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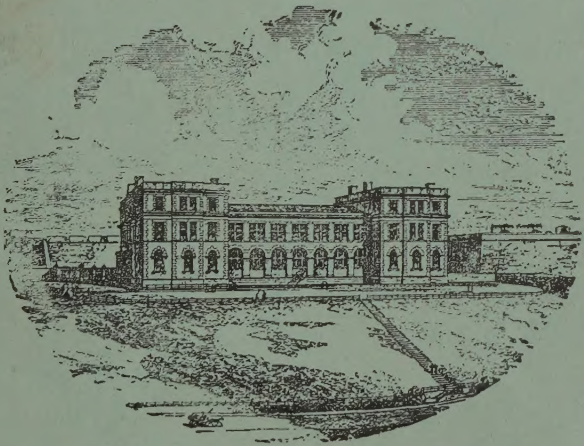

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Observations and Experiments on Sex-Change in the European Oyster (*O. edulis*). Part III. On the Fate of Unspawned Ova. Part IV. On the Change from Male to Female.

By

J. H. Orton, D.Sc.,

Department of Zoology, the University, Liverpool.

With Text-Figures 1 (Part III) and 1–7 (Part IV).

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PART III. ON THE FATE OF UNSPAWNED OVA.

AN analysis of the quantity and distribution of unspawned eggs in the gonad of *O. edulis* recorded in Table IV, **1**, 1927 (of oysters with young) and Table IX, **1**, 1927 (of post-spawned oysters), gives useful information regarding the occurrence and fate of unspawned ova as may be seen from the figures given in Table A.

TABLE A.

Group.	Developmental stage* of embryos or larvæ found in mantle cavity.	No. of *O. edulis* in each period.	Gonad of parent.				Totals with unspawned ova.	
			with few relict ova.		with ∞ relict ova.			
			no.	%	no.	%	no.	%
1.	Embryos (A+B+C) . .	205	122	*60*	46	**22·5**	168	*82·5*
2.	Ciliated and early shell stages (D+E)	241	113	*47*	28	**21·3**	141	*68·3*
3.	Coloured larvæ with bivalve shell (F)	256	54	*21*	8	**3·1**	62	*24·1*
	Totals . .	702	289		82		371	
	Table IX *loc. cit.*							
4.	Postsick† (G to J) . . .	444	13	*2·9*	11	**2·5**	24	*5·4*

These figures show an important sequence correlated with the lapse of time after spawning; thus few unspent ova occur in 60% and many unspent in 22·5% of individuals in Group 1, which have recently spawned (A+B+C), as is attested by the occurrence of only embryos in the mantle cavity. Many of these oysters spawned after the act of dredging, and may be considered to have spawned prematurely. Such individuals were doubtless on the point of spawning and some might have spawned if they had been left undisturbed, but it is probable that in a fair proportion spawning was precipitated by the act of dredging and the retention afterwards out of water.

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* See I, p. 983, for definition of these stages.

† Individuals carrying embryos or larvæ are designated "sick" by oyster-cultivators.

Those individuals (D+E) which were carrying ciliated or partially shelled larvæ (aged 3 to 4 days) had clearly spawned naturally on the beds before being dredged. Nevertheless 47% of them showed a few unspawned ova, and 21·3% many. Oysters with coloured and fully shelled larvæ (F), however, show only 21% with few and only 3·1% with many relict ova. After extruding their larvæ a total of 444 oysters (G to J) showed only 2·9% with few ova with the addition of only 2·5% with many unspent ova.

The decreasing percentages of unspawned ova in the parents correlated with (*a*) the increasing age of their larvæ and (*b*) the post-sick phase, clearly show that it is normal for unspent eggs to be voided from the gonad after the main act of egg-spawning. The sudden drop in the percentage between Group 2 (D+E) and Group 3 (F) is critical, since all the individuals in these groups spawned naturally on the beds; it indicates that the voiding of unspawned ova is effected largely at the time the parent is carrying well-developed larvæ. This process is continued after the larvæ are extruded, but appears to be still incomplete in 5·4%, of which 2·9% are negligible. The residual 2·5% of cases with numerous unspawned ova among post-sick phases are noteworthy.

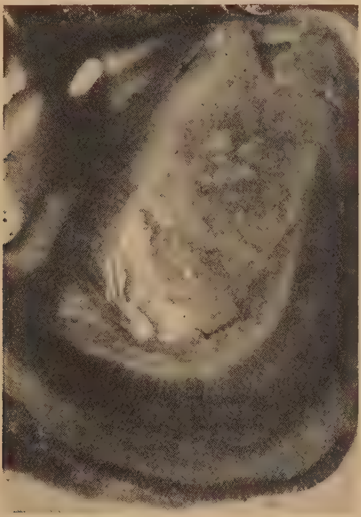

Fig. 1.—Photo of visceral mass of *O. edulis* living showing one large and several small patches of unspawned ova. The large patch is in the centre of the visceral mass. × *ca.* 2. (Photo by A. J. Smith.)

Confirmatory evidence of the extrusion of relict ova after spawning has been obtained in seasonal studies of oyster populations, but information so obtained is less easy to present and is perhaps less satisfactory than such convincing figures deduced from data already published—as are given above.

The different percentages obtained for Groups 1 and 2 in Table A are in part a measure of the differences resulting from premature and natural spawning, but since relict ova are shown to be extruded in bulk when the embryos are only a few days older (in Group 3) it is possible that this process may begin soon after the spawning act. In Table IV, *loc. cit.*, 12 instances are recorded of the occurrence of numerous to 70% unsegmented eggs occurring along with embryos in the mantle cavity, and many similar instances are recorded in **2**, 1927. It is probable that in these spawning individuals extrusion of unfertilised ova may have occurred after the main spawning act. In some cases fertilisation had occurred, so that larvæ of different ages were found together in one oyster. These facts already published confirm the deduction from Table A that relict ova may be voided from the gonad soon, i.e. within a few days, after the main spawning act.

In the event of relict ova remaining in patches in the gonad (see Fig. 1) the body of the oyster often presents an appearance to the naked eye designated as "curdley." It would appear that degeneration with absorption of these eggs usually and possibly always occurs.

Microscopic sections of a number of different types have confirmed observations on fresh material that degeneration usually occurs, but extensive exploration of preserved types is required to learn what happens in all circumstances.

In examining fresh smears of the gonad of oysters at the beginning of the breeding season when eggs are developing rapidly, the possible occurrence of new or old (i.e. last season's) relict ova is a disconcerting factor, and great care is needed in assessing the effective sexual condition of the material examined. There can be little doubt that mistakes have been made in this respect by both experienced and inexperienced workers.

The proportion of females found incompletely spawned while carrying young varies in different seasons, and is probably usually slightly higher at the beginning of the breeding season on most grounds. In Table IV, **1**, there are incompletely spent 65% (163) in June; 57·5% (256) in July; 45% (182) in August; 48·5% (95) in September; and 16·7% (12) in October. The numbers in brackets give the total examined each month, and the monthly grouping gives a close approximation to the course of the spawning season on the different beds whence material was obtained.

Abnormal incomplete spawning was found on the Fal Estuary beds in 1927 and is discussed in **2**, pp. 403–4.

SUMMARY.

An analysis is made of the records of unspent ova in the gonad of 1146 oysters (*O. edulis*) with—or recently with—young. High percentages of gonads with relict ova occur within a few days from spawning, much smaller percentages a few days later and still smaller ones one to two months after spawning. It is inferred that unspent ova are normally and mostly extruded from the gonad within a few days after spawning; confirmatory evidence for this view is adduced from published observations. It was found that masses of relict ova may be retained in the gonad for a longer period in about 2·5% of recently spawned females. It is pointed out that if these residual ova were fertilised upon extrusion they would give rise to a successful but spurious second spawning.

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1. Orton, J. H. Journ. Mar. Biol. Assoc., N.S., Vol. XIV, p. 967, 1927.
2. do. Nature, Vol. 120, p. 403, 1927.

PART IV. ON THE CHANGE FROM MALE TO FEMALE.

Review of Earlier Work.

Since the year 1920 the writer has been accumulating evidence on the problem of sex-change in the European oyster, *O. edulis*. In 1927 (**1**) the relevant literature on the subject was reviewed and an outline given of the observations and experiments being made with a view to obtaining critical information regarding sex-changes (**1**, p. 969). The first part of the projected programme consisted in the examination of the gonad of more than 1000 individuals at various periods after the extrusion of ova from the gonad. This part of the programme was accomplished by laboratory and field observations and by isolating proved and spawning females in tanks and in cages in the sea. The results of this work were published in 1927 (**1**), wherein it was demonstrated :—

(1) that among 702 individuals carrying young 97·3% were found in some phase of developing maleness ;

(2) that development of sperm-morulæ begins normally in the gonad of oysters within a few hours after the act of egg-extrusion ;

(3) that this development normally accelerates in the course of a few days, so that by the time the oyster is carrying black-coloured larvæ the gonad contains ripe sperm-morulæ (in many such individuals the gonoducts are also full of ripe sperm-morulæ ready to be discharged, see **2**, Fig. 1, p. 316.) ;

(4) that this phase of sperm-development attains a peak within one to two months after the act of egg-spawning and then wanes, *if spawning has occurred early in a normal season on a productive type of oyster bed*, e.g. West Mersea, River Blackwater, Essex; or Upper Fal Estuary; or Whitstable beds, Thames Estuary. The probability was discussed that this phase of sperm-development may be slowed down or arrested in the autumn and winter in individuals spawning as females late in the breeding season (see **3**, Table VI, category 21), and be completed in the following spring and early summer. Evidence on this aspect has since been accumulated and is presented in this paper.

(5) that a variety of intersexes (or mixed sexes) occurs, some of which can be recognised by naked-eye inspection.

In 1928 the breeding period of the oyster was discussed (**3**) in a general way in relation to spring and autumn periods of shell-growth (increase in shell area). In that paper (p. 399 and Table VI) is given an analysis of the sex-condition in October and November 1927 of some 1800 oysters from the beds in the Upper Fal Estuary. Thirty categories of individuals in different sexual or physiological conditions are recognised. A study in the seasonal variation of these categories during 1926 and 1927 has been made and will be discussed later in its bearing on sex-change in the population. In 1931 figures were published (**2**) of the gonad of the oyster at successive stages after the act of egg-spawning. Some results of experiments on the change of sex from male to female were given in the paper (**1**) (1927, lots 106 to 115B, pp. 1027 to 1033), but a discussion of the results was reserved for a separate publication. The portions of the original programmes of work dealing with the experiments on sex-change from male to female, **1**, p. 969 (*b*) and (*c*), are given in the following pages. A statistical investigation of seasonal sex condition in oyster populations from data already collected and extending over a period of three years is being undertaken along with other work, and a full discussion of the sex-physiology of the European oyster is reserved for a later publication.

INTRODUCTION.

During the period 1922–27 experiments were designed and carried out in the River Blackwater, in the River Yealm near Plymouth, and on the Fal Estuary to obtain evidence of the change of sex in individuals of *O. edulis* from male to female. These experiments have been partially successful inasmuch as this sex-change has been detected in a relatively small proportion of individuals (i.e. ranging from 10 to 50%). An ideal experiment should give sex-change in very nearly 100% of the animals. The change in sex from male to female is clearly not of the same automatic nature as that from female to male ; moreover, the recognition of a female phase will be lost if individuals spawn as females and evacuate their young in the interval between successive examinations of the experimental oysters, for such spawning individuals revert rapidly to the male condition as is now abundantly proved (**1**). The knowledge acquired in the course of these experiments would be used, it was hoped, to design more promising experiments on a larger scale, but the recent shortage of oysters on most English beds (**4**) has interfered with this project.

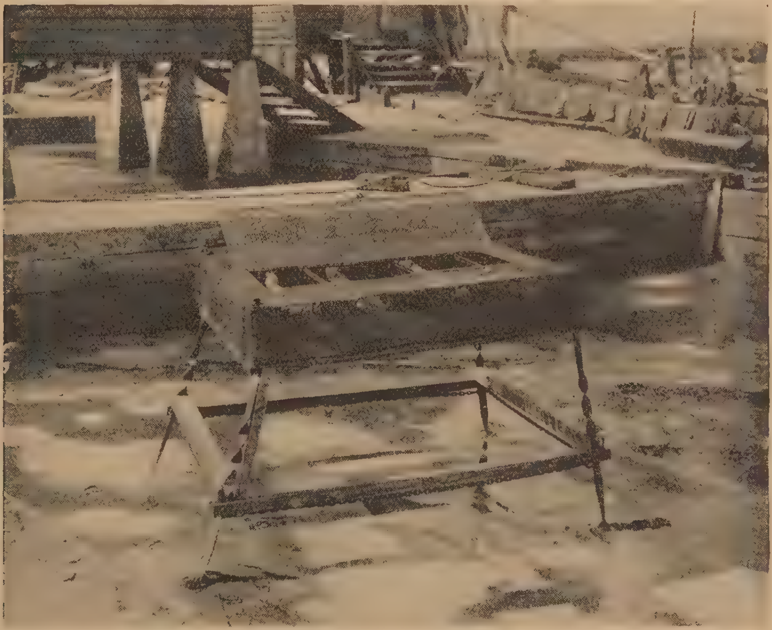

Fig. I.—View of the experimental oyster cage used at West Mersea, showing the oyster pits at low water.

The chief difficulty in carrying out experiments on change of sex in oysters lies in keeping the experimental individuals under healthy conditions while at the same time taking precautions to isolate them unimpeachably from others. The writer holds the view that for work of this kind, the animals should live under conditions as nearly natural as possible. It was therefore decided to fix the site of the experiment *on grounds where oysters form natural beds* so that there can remain no doubt of the suitability at least of available water and food.

In order to isolate the experimental material and render recovery easy, a large cage 6 feet by 5 feet by 10 inches deep made of iron wire mesh

($\frac{3}{8}$ inch in diameter) was designed and used for the work (see Fig. 1, p. 7). This cage was divided by permanent partitions into four compartments, two large and two small, so arranged that each compartment could be recognised without the provision of a label (see Fig. 2, p. 10). This device proved extremely useful in dealing with heterogeneous material. Oysters in a known sex-condition at a known time were placed together in one compartment; individuals were mostly easily distinguished by tracing the outline of the shell and adding drawings *in situ* of barnacles and other permanently attached growths; some shells not otherwise easily recognised were marked with a distinctive file-mark. In special cases a small cage was constructed and attached inside the large cage to isolate an individual. The practical difficulties of maintaining an experimental cage of this kind on a commercial oyster bed for a number of years are very great; it was only by the hearty co-operation and good-will of the Directors and employees of the Tollesbury and Mersea Native Oyster Company that experiments in the River Blackwater were rendered possible; the difficulties of experiments on the River Yealm near Plymouth were overcome by the personal interest of Mr. J. Kingcome and the Director of the Yealm Oyster Fisheries. On the Fal Estuary where the beds are public, experiments had to be confined to the summer period, when the beds are closed for general dredging; permission for these experiments was courteously given by the Truro Oyster Beds Committee and rendered possible by the help of Mr. E. Searle and many oyster-dredgermen.

MATERIAL.

The oysters used in these researches were obtained by dredging in the breeding season chiefly at West Mersea, River Blackwater. Some were also obtained from other English grounds, namely Fal Estuary, Whitstable, River Yealm, and the River Helford. The age of the experimental oysters varied from about 3 to 7 years, but was estimated at being mostly from 4 to 6 years. In the earlier years, from 1922, the average age would probably be greater than later when the larger individuals were becoming relatively scarce. It is a difficult matter to obtain large numbers of oysters carrying young without destroying these valuable molluscs. The writer was fortunate at West Mersea in being able frequently to examine catches of many thousands dredged for the purpose of relaying, and at the same time of following the course of the breeding season. On productive beds such as occur at West Mersea, it is desirable to find out each year when a significant proportion of oysters have reached the blacksick stage, in order to make preparations for putting out clean shell at a time which will coincide as nearly as possible with the probable settling time of the oyster larvæ. The examination for spawning oysters is therefore a routine operation, of which advantage was taken to collect as many young-bearing individuals as possible. When oysters with young are kept out of water for some time a proportion will often exude a few embryos or larvæ from the edge of the shell, having opened the shell presumably in response to some stimulus, such as the need to respire, whereupon a few of the young flow out of the shell with a little of the mantle liquor. It is possible that the embryos themselves provide the stimulus for the opening of the shell merely by exerting continuous unusual pressure upon sensitive parts of the mantle. Individuals suspected of carrying young may be tested as described on p. 15.

Early in the breeding season 1% of a sample may be detected as female spawners after exposure to air on warm nights, while later in the season as high a proportion as 7% may be found in this way.

On beds where oysters are not caught in bulk in summer the experimental oysters were obtained as is described on p. 15, or in process of opening large samples.

METHODS.

The experiments on sex-change from male to female were of two kinds :—

(A) A total of 313 individuals, proved to be male at the time of examintion (usually about July), were isolated at different times and places in one compartment of the cage and returned to the oyster bed (see Fig. 4, p. 13). These oysters were taken out of the sea after various intervals of time—usually about a year later—and tested at intervals during the ensuing spawning season for individuals carrying young. In this kind of experiment only those females which were actually carrying young at the time of examination could be detected. If individuals spawned and released their young during the interval between successive examinations, their sex-change would not be known. It was considered imperative to return the oysters to the natural habitat as soon as possible after examination in order to maintain normal and healthy conditions of growth and gonad development. Although sex-change was found in experiments of this kind there can be no doubt that the actual percentage of individuals undergoing sex-change was greater than was observed.

As a variation of this experiment samples of the material were opened at various intervals after the beginning of the experiment and examined macro- and micro-scopically for stages of development of femaleness.

The detection of males for experimental purposes was effected by examining the contents of the gonad extracted by means of a fine pipette passed through a boring made in the shell of the oyster (see Fig. 3, p. 11). Only those individuals were selected as " male " which yielded only sperm-morulæ. Hermaphrodite individuals and any others from which eggs as well as sperm-morulæ were obtained were rejected.* The individuals selected were therefore essentially passing through one or other of the male phases (see p. 16). The shell boring was made in the left valve from a position varying from postero-dorsal to sub-median (see Fig. 3). From this position the gonad can be tapped near the surface of the body (see **5**, 1924, Plate XII) with relatively little risk of damage. In some instances the intestine was perforated.

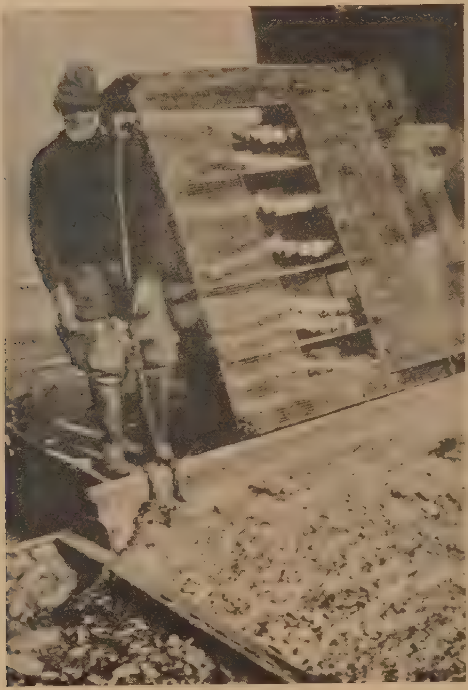

Fig. 2.—View of the experimenta oyster cage, dismantled and prepared with shells for catching oyster and Crepidula spat.

The experimental oysters mostly recovered easily and well from this operation (see pp. 18, 23), though doubtless some of the mortality which subsequently occurred was caused directly or indirectly from the operation. The boring in the shell was observed in some cases to be quickly sealed by deposition of a horny or calcareous membrane derived from the epidermis of the oyster; the body wound also healed quickly but sometimes formed a scar. In a few cases the perforation of the shell was so well sealed internally (see Fig. 3, B, D) that a drill had to be employed to expose the body again; usually the new shell was thin and could be broken with the assistance of a small steel instrument. Sympathetic deposits sometimes occurred on the right valve (see Notes, p. 25).

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* In Experiment 1 a few males with obviously relict ova were accepted.

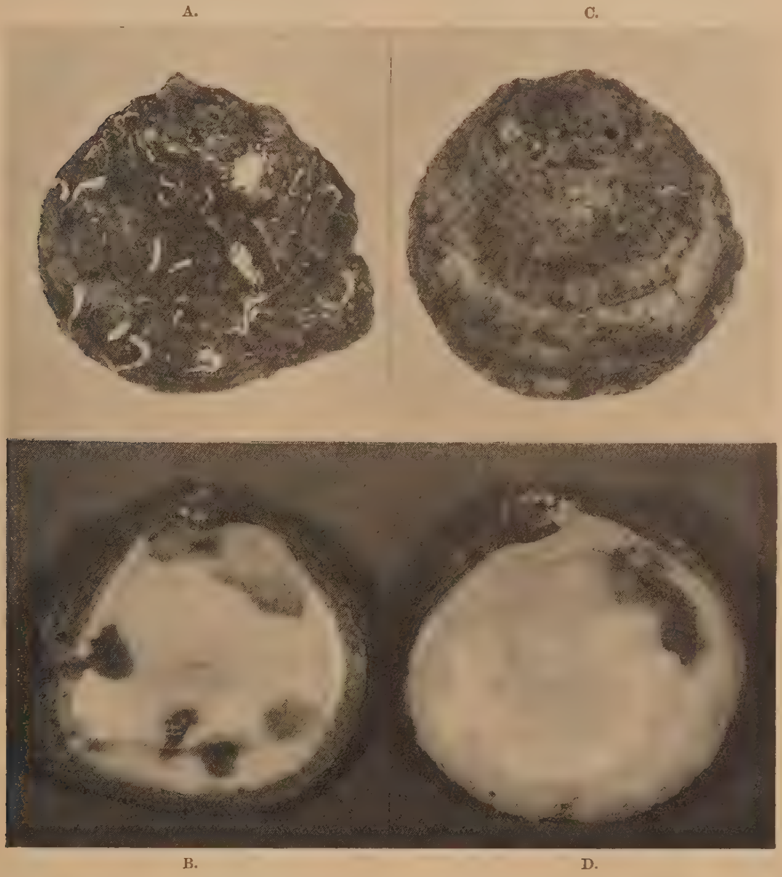

Fig. 3.—Views of external and internal faces of two bored left valves of *O. edulis* from Experiment 3. × *ca.* $\frac{5}{8}$. (Photos by P. Bond.)

A and B views of one valve. In A the boring is well shown near the umbo on the right. In B the site of the boring is near the umbo on the reader's left, and is covered with nacreous shell. The dark area extending from the boring is due to infiltration, but is little more than a stain on the shell itself.

C and D are views of another valve also showing perfect sealing of the boring internally. The site of the boring in D is near the umbo on the reader's left; the sealing is perfect.

(B) As adequate proof has been obtained that spawning females change normally—to the extent of 97%—into males immediately after the spawning act (**1**), it is sufficient to isolate individuals carrying young to obtain thereby a collection of males in the early stage of developing the male phase. Samples of oysters (amounting to a total of 663 individuals) bearing young were therefore isolated in compartments of the cage in the years 1922–25 and 1927, and kept in the sea for periods of months or years during which they were examined at intervals for the return of the female phase.

The reliability of this kind of experiment depends upon the degree of completeness of the egg-spawning act. There can be no doubt that the normal method of egg-spawning results in the extrusion of all or most of the eggs in the gonoducts and gonad at one and the same time (see **6**), although 50% of egg-spawners may retain a few to many scattered eggs in the gonad; nevertheless, the experience gained in examining more than 1000 spawning females, as well as many thousands of other specimens throughout the seasonal cycle of sex changes, indicates that *in a few cases* females incompletely spawned at the first attempt may spawn successfully again as a female within a period varying from a few days to more than a month. Successive spawnings of this kind, it will be noted, occur from one batch of eggs and do not involve two phases of egg-production. The fate of unspawned eggs is discussed in **1**, p. 976, and **6**, in this issue of this Journal; the significance of two acts of egg-spawning from one phase of egg-production will be discussed later with the results of the experiments.

On the Cage and Cage Operations.

The experimental cage with its addition of legs is shown in Fig. 1. Legs were found to be desirable to avoid the accumulation of mud which occurs even in an open iron wire-meshed cage lying on the bottom in such silty water as occurs in the Blackwater creeks. The meshes of the cage were $\frac{3}{8}$ths of an inch square. In the earlier experiments when the cage lay on the bottom a disastrous mortality and weakening of the oysters accompanied the accumulation of mud in the structure. The cage itself could be removed from the collapsible table structure and was conveniently placed in sea-water in the pit, shown in Fig. 5, p. 14, underneath the storeroom, which was used as a laboratory. As the experimental material was prepared it was transferred direct to its appropriate compartment in the cage and maintained conveniently in sea-water. During spring tides the sea-water in these pits is well and frequently renewed (see Fig. 5).* The compartments of the cage and central lid on one face —so constructed as to prevent loss of material in the event of the lid being forced open—with the strengthening rods and tubular corner sockets for

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* During neap tides it was noticed that *Ciona intestinalis* especially seemed to find conditions intolerable in these pits. As the water and aeration appeared to be good, the lethal condition suspected was the exposure to very strong sunlight.

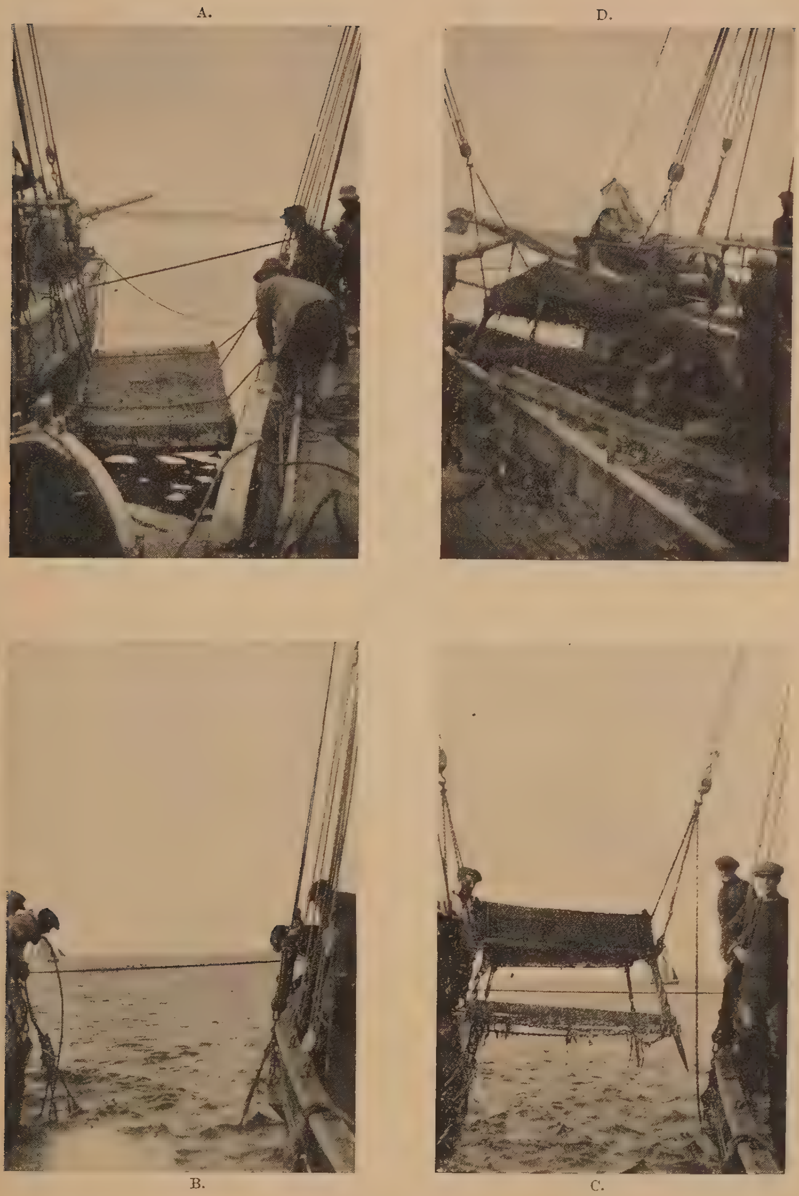

FIG. 4.—Four views of the operations in putting out and hauling the experimental cage.

A. The skiff has been withdrawn from below the cage, which is now being lowered into the water.
B. Hauling the cage after recovery of the anchors and chains.
C. Cage hauled clear of the water to permit the passage below it of the skiff.
D. Cage being lowered into skiff, preparatory to conveyance to the oyster-store.

the legs are seen in Figs. 1 and 2. Four narrow iron bars with end-holes fitting on the upper part of the legs formed a skeleton table on which the cage rested (see Fig. 1). The tops of the legs projecting through the corner sockets of the cage were threaded so that the cage could be secured by good bolts.

The cage was assembled on its table and the experimental material enclosed while the apparatus was on the foreshore, or in a large flat-bottomed boat, a skiff beached near by. At low water the skiff was towed to the Deeps (**9**, see Chart, Fig. 2) and manœuvred between two anchored and yoked dredging-boats. The cage was then hoisted by its anchor chains, which were secured to the legs, and the skiff removed (see Fig. 4, A, p. 13). Ropes were then run through pairs of handles on the top edges of the cage, and lowering gradually proceeded with until the bottom was reached. Bearings were then taken. The anchors, two in number, were run out separately, held and lowered by ropes until taut, when the rope was slipped and hauled in. A lead with line was left on the cage for testing the position of the cage at the end of the operations.

FIG. 5.—View of the oyster pits flooded at high water, showing the oyster store on the left used as a laboratory.

In hauling, the anchors were first creeped, then the two boats anchored in position with the cage anchors and chains aboard. The cage was then hauled and well washed; the skiff was run under it while clear of the water (see Fig. 4, B, C, and D). In a clean haul the cage could be dropped snugly into the skiff and taken at once to the store for further washing and examination of its contents. When the cage had lain undisturbed on the beds during the winter an accumulation of mud was *always* found in it. On the site of the experiment there was a depth of two fathoms at low water; the same site was used in all the experiments carried out at West Mersea, River Blackwater.

ON TESTING FOR INDIVIDUALS CARRYING YOUNG.

In testing for individuals incubating embryos or larvæ in the mantle cavity at the time of examination, the adults, after being washed or scrubbed, were usually laid out with the flat valve downwards on glass plates on a temporary bench in a room serving as a laboratory. In warm weather under these conditions oysters will often soon extrude a few embryos or larvæ at the edge of the mantle. The sample was usually left under these conditions overnight, covered in hot weather with a damp cloth, the young-bearing individuals being isolated in sea-water in shallow dishes as they were detected. On transferring young-bearing forms to water in a dish a certain number of the young are usually soon extruded into the water (see Fig. 6, above), thus permitting confirmation of the first indication of the gravid condition.

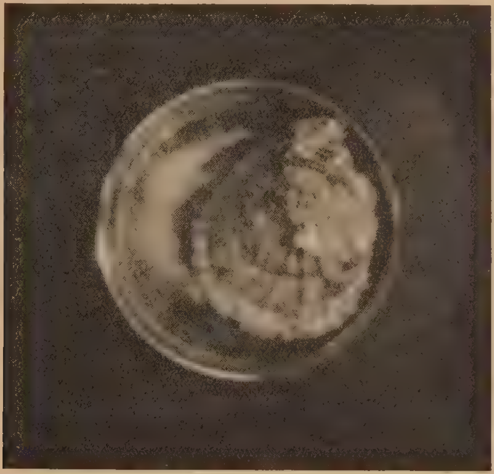

FIG. 6.—Photo of *O. edulis* found to be carrying young by the method of testing in small dishes—× ca. $\frac{1}{3}$. The white mass on the reader's left, concentric with the shell, is composed of hundreds of thousands of larvæ.

The oysters which failed to extrude larvæ on the bench were each again washed and isolated in a small dish of sea-water. The water in these dishes was renewed at intervals for one or two days, during which careful examinations were made. Usually the gravid individuals would evacuate a large portion of their young sooner or later, but sometimes the young were retained tenaciously. To detect these latter cases without injury advantage was taken of any such oyster opening its shell-valves widely to close the valves forcibly and quickly by hand-pressure. In this way a volume of water was suddenly expelled from the mantle cavity, carrying with it a number of larvæ if such were present. Widely open oysters could be examined by the naked eye.

This method of testing was efficient, but necessarily involved a constitutional strain on the material, especially when repeated after short intervals, and no doubt contributed towards delay in sex-development and the high mortality found during the experiments. A quicker method of testing, which avoids injurious effects, is desirable in future experiments.

ON THE DEVELOPMENTAL SERIES OF MALE SEX-PHASES.

In a study of the state of the gonad at various intervals of time after egg-spawning it was convenient to establish an arbitrary series of possible conditions of the gonad (**1**, p. 981). Ten such arbitrary categories in the condition of the gonad with regard to the development of sex-cells were instituted (*loc. cit.*). Among these ten categories, numbered in succession I to X, it was found that seven (numbers III to IX) form definitely a series of sex-phases in the development and history of maleness. This series is given below in Table B and renumbered I to VII. A stage VIII is recognised, in which all the male elements have been evacuated from the gonad. This stage is neuter, but is historically related to the male-phases, and is conveniently retained as No. VIII in succession to No. VII.

For convenience the old arbitrary category numbers are given against the serial numbers of the sex-phases.

TABLE A. THE DEVELOPMENTAL SERIES OF MALE SEX-PHASES.

No. of male sex-phase.		Sex-cells present in gonad. Ripe sperm-morulæ.	Developing sperm-morulæ.	Ripe unspawned ova.	Arbitrary Category. given in **1**.
I	waxing	none	a few to ∞ young up to 40 μ.	none or a variable no.	III
II		none	f. ∞ or ∞ over 40 μ.	do.	IV
III		few or f. no.	∞	do.	V
IV	ripening, or ripe with gonoducts filling or full	f. ∞ or ∞	f. ∞ or ∞	do.	VI
V		∞	f. no. to few	do.	VII
VI	waning	f. ∞ or ∞	none	do.	VIII
VII		f. no. to few	none	do.	IX
neuter =VIII		none	none	none or a variable no.	neuter =X

Abbreviations: no.=number; ∞ = numerous; f.=fair or fairly.

SERIES A.

Experiments on Oysters Proved to be Male.

Experiment 1. *West Mersea, R. Blackwater*, 1922.

The details of the first experiment in investigating the change of male individuals into female are given in Table I. One hundred and fifteen males were identified from June 28 to July 7, 1922, and put in the cage in the sea on July 8. The cage was left undisturbed and could not be examined until July 14, 1923, about one month after the breeding season had begun—when it was found to have become very heavily silted with mud, following heavy rains and much stormy weather. The accumulation of mud* had smothered most of the oysters and probably interfered with the normal development of those remaining. This experiment was regarded as a failure, and a new one begun at once; nevertheless, the surviving individuals were cared for and their sex-changes investigated.

Nineteen oysters survived the experience of the first winter, and of these four died in the summer following. None of the remaining fifteen were detected in a female phase from July 15 to August 2, nor from October 17 to 22, 1923. During the latter period oysters would not normally be expected to occur in spawn on the Blackwater beds, so that these oysters were in reality examined during the period of only two weeks of the spawning season. Some of these oysters may, therefore, very well have passed undetected through a female phase during the breeding season of the second summer†—which in this year began late, about the middle of June, and extended into August and possibly into early September.

Six specimens were tested on July 15, however, and found to be males. Nine others were put in the cage to winter again. On June 7, 1924, 2 of these were found dead, and another died soon afterwards. In the 3rd summer of this experiment 6 individuals only were left; 2 of these produced either embryos or larvæ; 1 was hermaphrodite and 3 were good males accumulating food reserves. One individual, carried through a third winter, was opened on July 16, 1925, again late in the breeding season, and found to be in the male phase.

Summary of Experiment 1.

Of 115 oysters proved to be males in July 1922, none were found to have developed a female phase in the next (2nd) summer. In the

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* A large number of *Ciona intestinalis* (up to 15 cm. long living contracted) and of *Ascidiella aspersa* (up to 7 cm. long living and extended) were growing on the oyster-shells and on the cage, having survived—but no doubt assisted in—the deposition of mud.

† The summer in which an experiment is begun is designated the 1st summer of the experiment; the summer in the following year is the 2nd summer; and the next following summer the 3rd summer of the experiment, and so on.

3rd summer, 3 of the surviving 6 individuals became ovigerous or larvigerous. The larvigerous individuals were found developing a new male phase.

Heavy mortality occurred among the experimental oysters in the winter of 1922–23, and examinations for female phases were made during only a part of the breeding season in 1923 and 1924.

Female phases may have been inhibited by the bad experimental conditions in 1922–23, and some may also have escaped detection in the limiting conditions of the experiment, i.e. the possibility of examining for individuals carrying young during only a portion of the spawning period.

TABLE I.

EXPERIMENT 1.

West Mersea, River Blackwater, on O. edulis *proved to be male.*
June 28th to July 7th, 1922.

Date.	Operations.	Dead in cage.	♂	♀ with young.	Un-spawned ♀	Total dead.	Total living.
July 8, *1922*	115 ♂'s put out in the cage in the sea						115*
July 14, *1923*	Cage hauled . . .	**96***					19
,, 15	4 individuals ♂ opened and preserved: 2 individuals A. ♂ phase V B. ♂ phase VI . .		4 (2)	?	?	100	15
15	15 individuals put again in the sea . . .						15
,, 23– Aug. 1	Oysters re-examined for ♀ spawning individuals—none found . .	2	?	?	?	102	13
,, 2	13 individuals put out in cage						13
Oct. 17	Cage hauled again . .	2				104	11
	No ♀'s in spawn, C. opened found in ♂ phase VI; D. opened, ♂ phase VIII		(2)	?	?	106	9
Oct. 22	9 oysters put in sea in cage						9
June 7, *1924*	Cage hauled . . .	2				108	7
,, 7–9	No ♀'s found in spawn .						
,, 9	Cage put in sea . .						7
,, 30	Cage hauled . . .	1				109	6
July 1–6	Oysters re-examined and finally opened, except one ♀ . . .	0	3*a*	2*b*	1*c*⚥	114	1
,, 9	One ♀-spawning oyster put back in sea . .						1
July 2, *1925*	Cage hauled . . .						
,, 16	Oyster opened; ♂ phase VI	0	1*d*	0	0	115	0

* Ninety-three of these shells were examined: 54 showed good recovery from the boring operation; 33 no recovery and 6 a bad recovery.

Notes to Table I.

(*a*) The condition of these three oysters was as follows :—

	Fish.	Growth of Shell 1923.	1924.	Length.	Recovery from Boring.	Sex-elements. Sperm-morulæ. Ripe	Unripe	Ova.
1.	Good	9–10 mm.	?	64 mm.	v. good	∞	fair no.	none
2.	F.g.	?	2–5	61	a boss of nacreous material projecting into tissues which have grown well around it.	∞	v. few	none
3.	Good	nil ?	2–5	65/82	perfect	∞	f. ∞	none

All three individuals were good male oysters accumulating reserve products.

(*b*) 1. One of these oysters extruded an enormous number of heliotrope coloured and shelled larvæ on July 1. The shell boring was opened and the gonad tapped and found to be developing maleness giving ∞ ripe sp. m., ∞ unripe sp. mor., and no ova (phase IV). On July 6 the gonad was again tapped and found to be male in a later phase (VI). The shell of this oyster was then marked with a file and put back in the sea on July 9. It was taken out of the sea on July 2, 1924, opened and found on July 16 to be in the ♂ phase VI (see *d*).

2. On July 6 the other oyster extruded during the night white embryos not ciliated ; this individual was opened on July 8 after two days in the sea and found to be in ♂ phase I with f. ∞ eggs left in spots in the gonad. It was therefore incompletely spawned but changing into the ♂ phase.

(c) 1.	Good	nil ?	5–10 v. thin	77	perfect	∞	none	∞ ripe

The gonad was of the type described as curdley : the individual had developed femaleness, and spawned incompletely as a female. This oyster had retained ripe sperm-morulæ whilst acquiring ova, and had become hermaphrodite, but a functional female.

(*d*) The "d" individual found with young in 1923 had a gonad in male-phase VI.

Experiment 2. *West Mersea, River Blackwater, and River Yealm, near Plymouth,* 1923.

In the second experiment with oysters proved to be male the following improvements were made in the cage and procedure with a view to diminishing the limitations.

(1) The cage was mounted on legs (see Fig. 1, p. 7) to enable the silt to fall through the bottom of the cage, which formerly had rested on the river bed.

(2) It was decided to visit the cage twice a year to overhaul and clean the cage and its contents.

(3) After examining the experimental oysters at the beginning of the breeding season on the Blackwater beds in the 2nd summer, it was decided to transport the experimental oysters to beds near Plymouth, whence they could be hauled at intervals during the same breeding season. In this way more opportunities would occur for detecting individuals at the instant they were carrying young.

The details of Experiment 2 are shown in Table II, p. 22. During the period July 24–August 1, 1923, 101 oysters were found to be male by examination of the contents of the gonad extracted by means of a fine pipette from the living animal through a boring made in the shell. These oysters were put in the cage in Deeps on August 2, 1923. On October 17, 1923, the cage was hauled for the purpose of cleaning away accumulations of mud and growths* and for examination of the oysters. It was found that the cage had overturned.

The oysters were, however, in good condition and had grown remarkably fine shell-shoots, as indeed had most of the oysters on the dredging grounds. Tests were made for spawning individuals, although the spawning season was considered to be finished ; no individuals were, however, found in spawn. A sample consisting of 18 of the experimental oysters was opened and examined (see note *a*, Table II). It was found that good recovery from the operations of boring and tapping had mostly been made : new shell-material had been laid down on the inside of the shell-perforation and effectively sealed the body from the external medium. Some individuals had made a poor recovery, but such might be expected to recuperate in the future. The mortality was low, amounting to 5%. The sample consisted of 10 neuter individuals, some of which were in poor condition, but others were accumulating food reserves normally, and 8 still in the male phase, but mostly in a waning male phase. None was found certainly in a female phase, though No. 11 may have had a few young ova in the gonad.

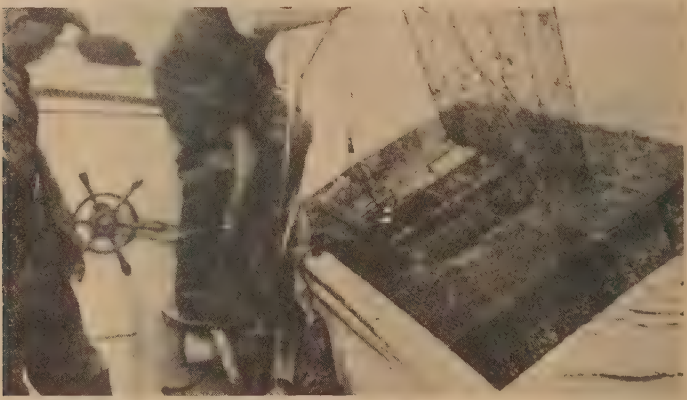

FIG. 7.—View of the smaller experimental oyster cage used in the R. Yealm being hauled from a motor-boat.

The remaining experimental material was returned to the sea on the Deeps bed on October 22, and hauled the following summer on June 7, when the cage was found upright, containing very little mud, and with a low mortality amongst the oysters. A very fine growth of colonies of *Alcyonidium gelatinosum* (commonly 10 cm. long) covered the top of the cage and served on this occasion—and on others—to show how the cage had been lying on the sea-bottom.

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* *Ciona intestinalis* up to 4·3 cm. long extended, *Ascidia conchilega* up to 2·5 cm. long extended and *medium Ascidiella aspersa* were found in numbers and removed. These animals are an important factor in the accumulation of mud in a cage.

At this time cold weather set in, and as none of the oysters were found in spawn on the day after hauling the cage, it was decided to put the cage back in the sea in Thornfleet Creek and examine it after a period of warmer weather. The cage was again hauled on June 30, and the oysters tested for females carrying young. Two such were found from July 1 to 6, and as it was thought that no others were in spawn, the whole sample was returned to the sea, pending its removal to Plymouth. Quick transport was arranged and the experimental oysters were put out in another cage in the oyster beds in the River Yealm on July 15. This cage was hauled on August 6 and the oysters tested August 6–8 for those carrying young. Two of such were found and the remainder put back in the sea on August 8. Again the cage was hauled on August 26 and, after testing, three more young-bearing females were detected. The remainder were again returned to the sea, but unfortunately a site could not be obtained on the proper oyster bed, and the most promising site near the dredging grounds had to be adopted. This site proved quite unsuitable (see note *h*, Table V); nearly all the oysters died during the following winter and the experiment was concluded.

Summary of Experiment 2.

One hundred and one oysters proved to be male on July 24 to August 1, 1923, were isolated in a cage in the sea in the River Blackwater on August 2, 1923. These were tested for individuals carrying young during October 17–22, 1923, and June 7–9, 1924; two oysters carrying larvæ were found in June. The experimental oysters were then transferred to a cage in the sea on the River Yealm near Plymouth. Further testing on August 6–8 yielded two more larva-bearing oysters; after another short period in the sea another test, made August 26–28, 1924, yielded three more larvigerous oysters, so that during 1924 7 individuals which were in a male phase in July 1923 had passed into a female phase and produced larvæ. Heavy mortality occurred in the remaining individuals in the winter of 1924–25 and the experiment was closed.

TABLE II.

EXPERIMENT 2.

On the Change from Male to Female: West Mersea, R. Blackwater, and R. Yealm near Plymouth.

Date cage put out. 1923	Cage hauled.	Remarks.	Dead in cage or opened.	♀ with young.	Total dead and opened.	Total living.
Aug. 2		In the Deeps oyster bed with 101 proved ♂ oysters				101
	Oct. 17		5			96
	Oct. 17–22	Sample examined; all tested	18*a*	0	23	78
Oct. 22		In Deeps			23	78
	1924					
	June 7		5		28	73*b*
	,, 7–9	Oysters tested		0	28	73
June 9		Cage put in Thornfleet				
	June 30	Cage hauled	4*c*	–	32	69
	July 1–6	Oysters tested	2*e*	2*d*	36	65
July		Oysters in sea temporarily	–	–	36	65
July 15		Oysters removed to Plymouth and put in cage in R. Yealm	4	–	40	61
	Aug. 6				40	61
	,, 6–8	Oysters tested at R. Yealm		2*f*		
Aug. 8					42	59
	,, 26		1		43	58
	,, 26–28	Oysters tested at R. Yealm		3*g*	46	55
Aug. 28					46	55
	1925					
	June 26	Experiment concluded	46*h*	0	92	9

NOTES ON TABLE II.

(*a*) A very good growth of shell (increase in area) was found in all the oysters except 19 on hauling the cage on Oct. 17. The new growth increased the height of the shell from 10 to 18 mm. and is described in **3**, p. 382.

The 18 individuals opened to obtain information on sex-change were found to show the following features on Oct. 18 to 21.

	No.	Length 1923 in mm. Aug. 3	Oct. 17	Recovery[1] of shell.	Fish.[2]	Gonad.	Ripe sp. m.	Unripe sp. m.	Ova.	Sex phase.[3]
	1	66	81	good	f.g.	undifferentiated	none	none	none	neuter
	2	50	67	do.	fair	not recorded	∞	do.	do.	♂ VI
	3	52	52	do.	f.g.	undiff.	none	do.	do.	neuter
gaping	4	51	59	poor	poor	do.	do.	do.	do.	do.
	5	48	48	do.	v.g.	n.r.	∞	a few	do.	♂ V
	6	53	53	perfect	v. poor	undiff.	none	none	do.	neuter
	7	62	69	good	do.	do.	do.	do.	do.	do.
	8	53	68	perfect	v.g.	do.	do.	do.	do.	do.
	9	60	68	good	do.	well dev.	∞	f. no.	fair no. relict	♂ IV
	10	58	68	perfect	fair	undiff.	none	none	none	neuter
	11	65	81	do.	f.g.	n.r.	∞	do.	few young ?	♂ VI
	12	69	87	do.	do.	do.	∞	few	none	♂ V
	13	76	86	do.	g.	do.	occ.	none	do.	♂ VII
	14	55	62	do.	fair	undiff.	none	do.	do.	neuter
	15	63	63	good	do.	n.r.	few	do.	do.	♂ VII
	16	70	76	do.	n. 0	do.	∞	do.	do.	♂ VI
	17	46	46	bad	poor	undiff.	none	do.	do.	neuter
	18	52	52	v.g.	do.	do.	do.	do.	do.	do.

(1) In 15 cases good to perfect recovery from the boring of the shell had been effected by sealing the boring from the inside with a nacreous deposit. In some of these shells, however, infiltration of foreign material had occurred, but this had been isolated on the shell and covered with a deposit of horny or calcareous material. When a poor recovery had been made these infiltrations were often extensive and had resulted in a great strain on the oyster in its effort to recover. In many cases the body showed a distinct scar opposite the boring where the gonad had been tapped.

(2) Under the term "fish" is given the relative condition of nourishment of the body as a whole; it is to be noted that a very good fish may occur in a neuter individual, e.g. No. 8.

(3) In these individuals in early male phases the gonoducts were full of ripe sperm-morulæ, in the older phases these were either empty or had few contents. In the neuter cases the ducts were often filled with a milky fluid which contained no sex-elements.

(*b*) On hauling the cage on June 7, 1924, 15 oysters had a new rim of shell-growth 3 to 8 mm., a slight growth only showed in 41, while no growth had occurred in 17.

(*c*) Of the four oysters found dead three had a slight recent growth of shell, 5 to 7 mm. in width, around the edge of the left valve.

(*d*) One oyster extruded into a dish ciliated larvæ on July 1; the next day the larvæ showed a trace of the larval shell and a tapping of the gonad showed the gonad to be in the ♂ phase I with a fair number of unspawned ripe ova. This individual was put in the sea and opened on July 8 when all the larvæ had been extruded. The gonad was found to be in ♂ phase III with relict ova in spots. Shell-recovery from the original boring had been perfect. Another individual extruded early embryo on July 6 at 7 p.m.; the next day the embryos at 11 a.m. were in the early heart-shaped stage and the gonad found in ♂ phase II with large sperm-morulæ ca. 110 by $30\ \mu$. Recovery from shell-boring had been perfect.

(*e*) Two gaping individuals were opened; one was neuter with muscle spindles (see **5**, p. 48) in the tissues, and the other in ♂ phase V with relict ova suggestive of recent female-spawning.

(*f*) Aug. 8. Black and shelled larvæ were extruded from two individuals whose gonads were in ♂ phase IV.

(*g*) On Aug. 27 one more oyster extruded black-shelled larvæ, and two similar cases were found the next day; all these oysters had passed into ♂ phase IV, as was found by retapping the gonad through the old boring.

(*h*) After the summer of 1924 the cage had to be moved off the dredging ground, and was placed in what was regarded as the most favourable place outside these grounds. The resulting mortality proved that the ground was entirely unsuitable. Periodical freshets and muddy water it is considered accentuated that weakening of the oysters which was no doubt caused by their removal in summer from West Mersea to Plymouth.

Experiment 3. *R. Yealm near Plymouth*, 1922.

Ninety-seven oysters proved to be male—from an examination of the gonad made through a boring in the shell—were put in the sea in a cage (see Fig. 7) on the oyster beds in the River Yealm on July 23, 1922. The experimental material consisted of 69 Yealm oysters (which are mostly relaid from Falmouth or Saltash), 20 from the River Blackwater (1922) and 8 Whitstables (1922). The cage was hauled on July 28 and 13 dead were found. A sample of the oysters was brought in for examination and found to be in good condition in good male phases (see note *a*, Table III). The rest were returned to the sea without delay. No further examination was made during the summer. In the spring the cage was visited for the purpose of cleaning and an unexpected accumulation of sticks and mud found in the cage with a concomitant very high mortality among the experimental animals. After a further examination on May 10 the cage was hauled and the oysters brought in on July 7 to be tested for female spawners. Only 19 individuals remained at the beginning of the spawning season of 1923. From July 7 to 10 two individuals were found with young embryos ; one of these yielded but few embryos, it is interesting to note. On July 9, 4 oysters were re-tapped and found to be in male phases ; their shells were marked with a distinctive file-mark ; 2 others were opened and found to be male and neuter respectively. The cage was hauled again seven weeks later (on August 30), when 4 more dead were found ; the remaining living were again tested for females with young. One such individual extruded numerous black-shelled larvæ and was found to have a filework on its shell. This oyster had therefore passed into a female phase since July 9 ! (See, however, pp. 26 and 42.) On September 4 the gonad of this specimen was again tapped and found to be in male phase V. The survivors, now reduced to 10, were again tested unsuccessfully for larvigerous individuals on September 11 and October 1.

On overhauling the cage on December 8 seven more dead were found and the remaining 3 failed to survive to the breeding season of 1924.

Summary of Experiment 3.

Of 97 oysters proved to be male in May–June 1922, 6 were found to be still in male phases in July 1922. No observations were made on the remainder for young-bearing individuals during the breeding season of 1922. Only 19 oysters survived to the winter and 4 more died during the following summer. Tests were made four times during the breeding season of 1923 for young-bearing females and 3 such individuals found. None survived the winter of 1923–24. One oyster carrying larvæ on August 30 had been proved to be male seven weeks earlier, on July 9.

Summary of Three Experiments on Sex-change in samples of Male Oysters.

It is advisable to consider the results from these experiments apart from those obtained in a second series which is described later.

When the results of these experiments are brought together as in Table IV below, it is seen that in the second summer of Experiments 2 and 3, 10% to 16% of the male oysters *were detected* in the act of carrying young. When it is considered that the breeding season may extend over about three months, and that oysters normally carry their young only from 6 to 14 days, it is highly probable that many of the experimental oysters passed through a female phase undetected. In Experiment 1 it is probable that female phases had just been experienced when the first test was made, and only one other test was made in the second summer. In the third summer of this experiment out of the remaining 6 individuals 3 (50%) were in a female phase.

The evidence obtained from these experiments offers definite proof

TABLE III.

Experiment 3.

On the Change from Male to Female, R. Yealm near Plymouth.

Cage put out.	Cage hauled.	Remarks.	Dead in cage or opened.	Female with young.	Total dead & opened.	Total living.
1922						
June 23		97 oysters proved ♂				97
July 28	July 28	Sample of 6 brought in and	**13**			84
		opened July 31	6*a*	–	19	78
	1923					
March 12	March 12	Cage examined and put out again	**55***b*	–	74	23
May 10	May 10	do.	**1**	–	75	22
	July 7	Oysters tested ; 4 rebored ;	**3**		78	19
		2 opened	2*d*	2*c*	82	15
July 10		Oysters returned to sea				
	Aug. 10	Oysters tested	**4**	1*e*	87	10
Sept. 4		Returned to sea	–	–	87	10
Sept. 11	Sept. 11	Tested oysters	0	0	87	10
	Oct. 1	Tested oysters	0	0	87	10
Oct. 16		Returned to the sea	–	–	87	10
Dec. 8	Dec. 8	Examined cage	**7**	–	94	3
	1924					
	June 24	Experiment finished. The 3 survivors died later	**3**	–	97	0

Notes on Table III.

(*a*) Six individuals showed the following features on July 31, 1922.

No.	Boring.	Fish.	Ripe sp. mor.	Unripe sp. mor.	Relict ova.	Sex-phase.
1	Covered ; partly calcified	v. good	∞	f. ∞	none	♂ IV
2	Covered ; beautifully calcified	do.	∞	none	rare	♂ VI
3	Covered ; partly calcified	do.	∞	rare	none	♂ V
4	Covered ; horny	good	∞	f. no.	do.	♂ V
5	Covered ; partly calcified	f. good	∞	∞	do.	♂ IV
6	Two borings both covered ; partly calcified	v. good	∞	f. ∞	few	♂ IV

It was noted that sympathetic deposits were present in all cases on the right valve in a position corresponding to that called forth to cover the boring on the left valve : in one case the deposit was noted to be partly calcified.

(*b*) Heavy mortality had occurred from a great accumulation of sticks and mud.

(*c*) On July 8 one oyster extruded numerous eggs in late segmentation stages. On July 9 another individual extruded a few eggs also in late segmentation stages ; upon opening this oyster the gonad was found empty : it is presumed that most of the larvæ had been extruded during the hauling process.

(*d*) The gonad in 4 individuals was re-examined on July 9 by breaking through the old boring ; one was in the male phase IV, two in V, and one in VI. The shells of these rebored individuals were marked with a cross by means of a file. Two weakly individuals were opened ; one was neuter and the other feebly ♂ V.

(*e*) One oyster marked with a cross extruded on August 31, 1923, numerous black-shelled larvæ ; this oyster had been proved to be male as recently as July 9, 1923. On September 4 the boring of this oyster was again opened and the gonad tapped, yielding a few ripe sp. mor. and numerous unripe ; it had thus attained again the male phase No. III.

that oysters pass from the male phase into the female phase in significant numbers. As the male oysters were taken at random from a population, it is not known how long such individuals had already existed in the male phase.

Evidence of sex-change from male to female in one summer was obtained in one instance, but such a rapid change was unexpected, and these experiments were not conducted with a view to detecting such a rapid development of the female phase. Evidence of the occurrence of successive male and female phases in successive summers is given by 10% to 16% of such changes in Experiments 1 and 2. Fifty per cent of the few survivors (6) in the third summer of Experiment 1 showed passage into the female phase in that summer, but the experimental conditions in this case were such as might be expected to cause delay in egg development.

The severity of the experimental conditions is clearly shown by an average total mortality of 65% before the advent of the second summer. It is therefore reasonable to suppose that more rapid changes are likely to occur in oysters lying free and naturally on the oyster grounds. The sex-changes observed experimentally are factual, but do not necessarily represent all the changes undergone ; neither does the period intervening between successive sex-phases necessarily represent the minimum period ; it is highly probable that the normal may be shorter than the observed period. Finally, the absence of records in sex-change in individuals in the second summer may be due either (1) to the detrimental effect of the whole of the experimental conditions (e.g. boring, tapping, muddy environment, repeated exposure in testing) or (2) to the passing of female phases during periods when the oysters were in the sea between successive periods of testing, or (3) to the intervening period being too short to permit the completion of those phases occurring between one egg-bearing phase and the next. The close analysis of young-bearing individuals with regard to the fate of their unspawned ova, given in **6** in this Journal, has an important bearing on these experiments. The effect of that analysis is to reveal the possibility that an oyster, presumably proved to be male by a tapping of the gonad, may nevertheless give spurious spawning as a female, if masses of relict ova occur in some other part of the gonad, and if these ova are extruded and fertilised. The possibility of this chance—i.e. a second spawning from one batch of eggs—occurring in females which spawned the previous summer is on the evidence available remote ; the possibility of the chance occurring in the same season is, however, on the evidence available 2·5 in 100, but it is advisable to double this number and regard 5 in 100 as possible in the discussion of results. Thus isolated cases of sex-change from male to female *in one season*—as in the instance noted above—must be regarded as non-significant if female-spawning could have occurred in the same breeding season. In the three experiments described above sex-change was rarely investigated in the first summer (see Table IV, below).

CONCLUSIONS.

Under such environmental conditions as occur on English oyster beds, it is found by experiment that oysters proved to be male in a given breeding season change to functional females in significant numbers (10 to 16%) in the next breeding season. Under wholly natural conditions it is highly probable that the percentage of males changing into functional females within a period of one year is much greater than that found under experimental conditions.

TABLE IV.

SUMMARY OF THREE EXPERIMENTS WITH SAMPLES OF MALE OYSTERS.

	1st Summer.			2nd Summer.			3rd Summer.		
	No. of oysters.	No. of tests for ♀'s	No. of ♀'s found	No. of survivors.	No. of tests for ♀'s.	♀'s found.	No. of survivors.	No. of tests for ♀'s.	♀'s found.
Expt. 1	115	*0*	0	19	*2*	0	7 (1 died)	*2*	3 (50%)
,, 2	101	*0*	0	73	*4*	7 (ca 10%)	9	*0*	—
,, 3	97	*1/14**	0	19	*4*	3 (ca 16%)	nil	—	—

TABLE IV*a*.

NUMBERS OF ORIGINAL MALE-PHASES IN EXPERIMENTS 1, 2 AND 3.

Sex-phase	II	III	IV	V	VI	VII	Totals.
Expt. 1	–	3	36	62	17	–	118 (3 died)
,, 2	–	2	44	34	18	3	101
,, 3	1	1	26	54	12	1	95+2 n.r.†
Totals	1	6	106	150	47	4	314

SERIES B.

EXPERIMENTS WITH OYSTERS BEARING YOUNG.

In the following series of experiments individuals found carrying either embryos or larvæ (see p. 15) were isolated in compartments of the cage and returned to the oyster beds to permit normal development of the succeeding sex-phases. It is known that the male phase is assumed immediately after egg-spawning, so that the samples dealt with here would all (but see discussion on p. 26) be males after extruding their

* 6 individuals opened July 31.

† n.r.=not recorded.

larvæ. The precaution was, however, observed in the later experiments of isolating whitesick individuals (i.e. those carrying young embryos or trochophore larvæ) separately from the blacksick ones (i.e. carrying coloured and shelled larvæ) even when both categories of oysters were found with young at the same time. Observations on this material were made as follows :—

(1) At various intervals after immersion in the sea samples were *opened* and the condition and sex-phases recorded.

(2) At intervals in the breeding season following that in which the experiment was begun, the oysters were taken out of the sea and *tested* for individuals carrying young at that time. After the test the remaining oysters were returned to the sea and again submitted to the same test after a short interval. Tests and immersions of this kind were repeated as frequently as desirable and possible during the breeding season of successive years. A preliminary account of the earlier experiments was given in 1922 (**8**).

Experiment 4. *On Females Bearing Young* (1922), *West Mersea, R. Blackwater.*

The first experiment with oysters carrying young was begun on July 8, 1922 ; details are given in Table V. Seventy-eight individuals found with embryos or larvæ between June 28 and July 7, 1922, were put in the sea in the cage on the Deeps oyster bed (**9**). The cage was hauled late in the breeding season of 1923, i.e. on July 14, when out of 32 living oysters 1 individual was found carrying young. Two other tests for gravid females were made in July without positive result, before the cage was returned to the sea on August 2. The cage was hauled on October 17 for cleaning and returning on October 22. In June 1924 19 oysters remained to be tested and 3 of these died in June. Of the 16 remaining specimens (see note *c*, Table V) 1 was found carrying embryos on July 6 ; 2 were fully ripe females ready to spawn ; 1 other was a ripe female dying, while 3 showed evidence of a recent female phase by the presence of relict ova in the gonad ; 8 others were good males and the 1 remaining was neuter.

Summary of Experiment 4.

Of 78 individuals found to be carrying young in July 1922, only 32 survived until July 1923. Tests for gravid oysters were not made at the beginning of the breeding season in 1923, and only 1 oyster with young was found in three tests made in July 1923. No other tests were made until June–July 1924 ; the remaining 16 oysters were opened on July 5–6, 1924, when 1 more gravid and 3 ripe females were found : 3 other individuals bore evidence of a recent female phase. In this experiment with individuals which all bore young in 1922, 1 again carried young in 1923, 1 was found with young in 1924, and 2 or possibly 3 were ready to spawn ova in July 1924. Three others in July 1924 showed evidence of having recently passed through a female phase.

TABLE V.

Experiment 4.

On Females Bearing Young (1922), *West Mersea, R. Blackwater.*

Cage put out.	Cage hauled.	Remarks.	Dead in cage or opened.	♀ with young.	Total dead & opened.	Total living.
1922						
July 8		Bearing young, June 28 to July 8, 1922	–	–	–	
		Cage put out in Deeps				78
	1923					
	July 14		**46**			32
	July 14–15	Tested; 6 opened	5*b*	1*a*	52	26
July 15		In sea in creek	–	–	52	26
	July 23	Tested		0	52	26
	July 31	Tested again	**1**	0	53	25
Aug. 2		In Deeps	–	–	53	25
	Oct. 17		**3**	0	56	22
Oct. 22			–	–	56	22
	1924					
	June 7		**3**	–	59	19
	June 7–9	Tested; 2 opened	2*c*	0	61	17
June 11	June	In sea in creek	–	–	61	17
	June 30	Tested	–	0	61	17
July 2		In cage in pit		–	64	14
	July 5–6	Tested and opened all; found 4 ripe females and 3 in recent ♀ phases	**3** 13*c*	1*c*	78	0
		Experiment finished.				

Notes on Table V.

(*a*) One other found greysick July 14, 1923: opened July 15/23 and found in ♂ phase V with patches of unspawned ova. The shell showed a growth of 12 mm. new shell at the ventral edge.

(*b*) Five oysters were opened and found as follows:—

			New shell growth ventrally.	♂ phase.	Length of shell.
1.	ripe ♂	ducts full	6 mm.	V	
2.	do.		6 mm.	IV	
3.	waning ♂ fair fish		nil	VII	70 mm.
4.	waning ♂	poor fish	8 mm.	VI	65 mm.
5.	waning ♂	good fish	7 to 9 mm.	V	65 mm.

(*c*) Two oysters found gaping on June 8, 1924, were opened and the 14 remaining opened on July 5–6, 1924. Their condition and sex-characters are as follows: 9 showed slight new shell growth from a trace at the exhalant aperture to a rim of 8 mm. of very thin shell at the ventral edge.

	Length in mm.	Fish.	Gonoducts.	Ripe sp. m.	Unripe sp. m.	Ova.	Sex-phase.
1.	80	f. good	full	none	none	∞ deg.	♀→ϕ
2.	60	v. poor	empty	do.	do.	small patches relict	♀→ϕ
	5.7.24						
3.	64*	poor	do.	do.	do.	none	ϕ
4.	60	good	f. full	v. ∞	do.	do.	♂ V
5.	67*	do.	empty	∞	a few	f. no.	♂(♀)A
6.	71*	v. good	do.	fair no.	none	∞ ripe	⚥
7.	49	do.	do.	none	do.	do.	♀
8.	79*	do.	do.	∞	∞	none	♂ IV
9.	73*	fair	f. full	∞	∞	do.	♂ IV
10.	62*	v. good	do.	∞	f. ∞	do.	♂ IV
11.	64*	good	empty	f. ∞	f. ∞	do.	♂ IV
12.	58–72	poor artery	do.	v. few	occ.	do.	♂ V
13.	57	good	do.	∞	do.	∞ deg.	♂(♀) B
14.	62*	do.	do.	∞	∞	none	♂ IV
15.	58	v. good	n.r.	∞	f. ∞	do.	♂ IV
16.	58*	good	full on left	none	occ. v. young	∞	♀–♂ I

No. 16 extruded embryos in late segmentation stages; when opened it was found to have spawned the eggs from the right side of the body only, the left remaining full of ripe ova. The gonad on the right had a curdled appearance due to many small patches of unspent ova. The individual had spawned incompletely some 12 to 18 hours before examination.

Experiment 5. *On Females Bearing Young* (1922). *Relaid R. Yealm.*

During June 16–22, 1922, 27 oysters recently forwarded to Plymouth from Whitstable, Port Navas, and the River Yealm, were found to be carrying embryos (whitesick). These were kept in the tanks at Plymouth until put out in the Yealm cage on June 23. Details of the experiment are given in Table VI, p. 31. The cage was hauled five weeks later when 2 oysters were found dead: 10 were brought back to the Laboratory and opened for information regarding development of gonad; 1 of these was found blacksick, carrying a large number of larvæ.

On March 12, 1923, the cage was hauled for cleaning; 10 individuals were found dead. The remainder were tested four times during the breeding season of 1923, but none found with either embryos or larvæ. None of these survived to the following breeding season.

Summary of Experiment 5.

Ten of the orginal 27 oysters used in the experiment were opened after being in the sea five weeks. One of these was found blacksick and had either retained its larvæ or spawned a second time from the eggs matured in June. Ten of the 15 remaining oysters died during the following winter and none of the survivors was found in spawn during four tests made in the succeeding breeding season.

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* Nine individuals showed a slight new growth of shell, June 7–9, consisting of very thin shoot varying from a trace at the exhalant aperture to a rim of about 3 to 8 mm. at the ventral edge. The gaper, No. 1, and several others had grown good shell-shoots in the autumn of 1923.

TABLE VI.

EXPERIMENT 5.

On Females Bearing Young (1922), *R. Yealm near Plymouth.*

Cage put out.	Cage hauled.	Remarks.	Dead in cage or opened.	♀ with young.	Total dead & opened.	Total living.
	1922					
June 23						27
	July 28	Tests made	**2**	–	–	25
		10 opened and examined	10*a*	1	12	15
	1923					
March 12	March 12		**10**	–	22	5
May 10	May 10		0	–	–	5
	July 7	Tests made	0	0	–	5
July 10			0	–	–	5
	Aug. 30	do.	**1**	0	23	4
Sept. 4			0	–	–	4
	Sept. 11	do.	0	0	–	4
Sept. 15						
	Oct. 1	do.	0	0	–	4
Oct. 16			0	–	–	4
	Dec. 8		**2**	–	25	2
1924	June 24	Experiment ended	**2**	0	27	0

(*a*) All these individuals were in either No. V or No. VI male phases. See **1**, Table IX, lots 92 and 93, for details of 8 of these oysters.

Experiment 6. *On Females Bearing Young* (1923), *W. Mersea, R. Blackwater.*

In this experiment 29 *O. edulis* carrying either embryos or young were detected between July 14 and August 2, 1923, at West Mersea and returned to the sea in Deeps in the cage on August 2, 1923. Details of the experiment are given in Table VII, p. 32. After a cleaning inspection in October 1923 the cage was hauled again on June 7, 1924, when 23 living oysters remained. A test made in June revealed no individuals bearing young, but early in July 2 such individuals were found. The survivors were opened on July 8, eleven months after the experiment began, when 1 more individual was found with embryos, 1 ripe female was ready to spawn, and 3 contained ova which were regarded as unspent from a previous female phase.

Summary of Experiment 6.

In 1924 3 oysters which bore young in 1923 were again found in good female phases (2 with young and 1 full of ripe ova) in July. This experiment was begun with 29 individuals, of which 20 survived to be examined in the following breeding season.

TABLE VII.

EXPERIMENT 6.

On Females Bearing Young (1923), *West Mersea, R. Blackwater.*

Cage put out.	Cage hauled.	Remarks.	Dead in cage and opened.	Ripe ♀.	♀ with young.	Total dead & opened.	Total living.
1923							
Aug. 2		In Deeps					29
	Oct. 17		1		0	1	28
	Oct. 20	Opened 2	2*a*		–	3	26
	Oct. 22		–		–	3	26
1924							
	June 7		3			6	23
	June 8	2 gaping; opened	2*b*		0	8	21
June 9		In Thornfleet	–	–	–	8	21
	June 30		3	–	–	11	18*c*
	July 1	1 gaping; opened	1	–	–	12	17
	July 1–2	Tests made	–	–	0	12	17
July 2		In cage in pit					
	July 5	Tests made	0	–	2*d*	14	15
	July 8	Remainder opened	15	1	1	29	0

Experiment ended.

(*a*), (*b*), and (*c*) are described in **1**, pp. 1027–8, Table IX, lots 107, 108, and 110.

(*c*) Amongst the 18 oysters opened and examined from July 1 to 8, 13 were in good male phases, two were found with numerous embryos or larvæ, one was a ripe female, and three others retained in their gonad ova which appeared to be degenerating and may be regarded as relict from the last female spawning.

(*d*) One of these individuals was a doubtful spawner: a few black larvæ were discovered on the glass plate below the oyster, but none were found in the mantle cavity.

Experiment 7. *On Females Bearing Young* (1923), *R. Yealm, near Plymouth.*

Experiment 7 was begun with 21 oysters received at Plymouth from various oyster grounds during June, July, and August 1923, and proved to be carrying young. Most of them were in the whitesick stage on arrival, but a few of the later ones were blacksick or bore shelled larvæ. Eighteen were sent from Whitstable, 2 from Port Navas, and 1 from West Mersea; whitesick individuals were received from the three localities between June 18 and 21. After being proved these oysters were kept in the tanks in the Plymouth Laboratory until put out in the experimental cage on August 30.

The cage was hauled on October 2 and a sample of 8 brought back to the Laboratory for the purpose of photographing the new good shell-growth made by the experimental oysters (see note *a*, Table VIII). When the oysters were again examined on June 24, 1924, 19 survivors were found and 1 extruded numerous embryos. Two more were carrying abundant young at another test made July 15–16, and 1 more was found at the fourth test made on August 8. Although these oysters had been relaid from various parts of England, 17 out of 21 survived a winter and the following summer. Only 1, however, survived the second winter.

Summary of Experiment 7.

Of 21 oysters carrying young in 1923 and relaid in the River Yealm on August 30, 1923, 4 were found again with young during the summer of 1924.

TABLE VIII.

EXPERIMENT 7.

On Females Bearing Young (1923), *R. Yealm near Plymouth.*

Cage put out.	Cage hauled.	Remarks.	Dead.	♀ with young.	Total dead or opened.	Total living.
	1923					
Aug. 30		On the Yealm oyster beds	–			21
	Sept. 15	Tests made	0	0	0	21
Oct. 16	Oct. 2–16	Sample of 8 brought in. Tests made; shell-growth good (*a*)	0	0	0	21
Dec. 8	Dec. 8	Cage overhauled	0	–	0	21
	1924					
	June 23	Tests made	**2**	1*b*	2	18+1*
June 26						18+1
	July 15–16	Tests made	0	2*c*	2	16+3
July 18			1	–	3	15+3
Aug. 8	Aug. 6–8	Tests made	0	1*d*	3	15+3
	Aug. 26		0	0	3	15+3
Aug. 28		Tests made	**1**	0	4	14+3*
	1925					
	June 26	Experiment ended	**13 +3**	0	20	1

NOTES ON TABLE VIII.

(*a*) A photograph of these 8 oysters is given in **3**, p. 381, with a description on p. 382. The new shell-growth varied from a few to 8 mm. in extent.

(*b*) This oyster extruded numerous embryos on June 24, in late segmentation stages, and was traced and put back in the cage. On July 16 the gonad was tapped and found to be in male phase V.

(*c*) One individual extruded numerous embryos at the instant of developing cilia and acquired a good ring of cilia by July 18. The gonad was retapped on July 17, and found to be in male phase I.

The other extruded numerous embryos in a similar stage; these also developed cilia and could swim on July 17. The gonad was in male phase I on July 18 and contained some unspent ova. Both oysters were traced and put back in the cage in the sea. On August 28 both borings were found to have been repaired. These oysters died during the following winter.

(*d*) One extruded numerous slate-coloured larvæ with shells 180 to 190 μ: on opening it was found to have a gonad in male phase III and to be completely spent (as a female).

* Individuals which spawned again in 1924.

Experiment 8. *On Females Blacksick, July* 1924, *West Mersea, R. Blackwater.*

From July 1 to 9, 1924, 60 blacksick oysters were proved and put out in the cage in Deeps on July 9. On July 2, 1925, the cage was hauled and 21 dead individuals found. The 39 living were tested unsuccessfully, July 2–5, for sick individuals and were put back in the sea from July 5 to July 13. On the latter date they were taken out of the sea and all opened during the following two days. The characters of these oysters at this time are given in detail in **1**, p. 1028, lot III, and are summarised as follows :—

TABLE IX.

1925	No.	Sex-condition.	Fish.
July 13–15	4	Carrying embryos or larvæ	poor to fair*
	1	Ripe female ready to spawn	very good
	12	Male phase IV	fair to good
	10	,, ,, V	poor to good
	8	,, ,, VI	poor to good
	3	,, ,, VII	poor to good
	1	macerating	
	39		

Experiment 9. *On Females Whitesick, June–July* 1924, *West Mersea, R. Blackwater.*

From July 10–13, 1924, 72 oysters were proved to be whitesick and stored in a pit. On July 8–9, 3 more whitesick individuals were found and all were put in the cage in the sea in Deeps on July 9, 1924, at the same time as those used in Experiment 8.

On hauling the cage on July 2, 1925, 49 living oysters were found. These were tested July 2–3 and 1 found blacksick ; 4 found gaping were opened and examined. From July 5–13 the sample was re-examined, when one was found dead ; the remainder were tested and opened July 13–16. The details of the examination are given in **1**, p. 1029, lot 112, and may be summarised as follows :—

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* Two had retained a few unspent eggs in the gonad. Only one individual among the 33 male phases had eggs in the gonad ; this individual had a gonad of curdley appearance, and the eggs were regarded as relict from a previous female phase. The cage was hauled after the beginning of the breeding season, it is to be noted, when early female spawners may already have extruded their larvæ.

TABLE X.

No.	Sex-condition.	With unspent ova.	Fish.
3	Carrying embryos or larvæ	1	poor to fair
0	Ripe females	0	
3	Male phase IV	0	poor to fair
13	,, ,, V	0	poor to v. good
21	,, ,, VI	2	poor to v. good (mostly fair to good)
3	,, ,, VII	1	fair to good
5	,, ,, VIII=neuter	3	poor to good
48		7	

In this experiment six individuals in non-functional female phases had retained few or many eggs from a previous female phase. As in the case of Experiment 8 some individuals may have spawned and evacuated their young in the early part of the breeding season of 1925, before the cage was hauled.

Experiment 10. *On Females* (*West Mersea and Fal Estuary*) *Blacksick, July* 1925, *West Mersea, R. Blackwater.*

A. During July 1925 a collection was made of 38 blacksick oysters from dredgings from the West Mersea beds. These were put out in the cage in Deeps on July 21, and hauled July 3, 1926. Twenty-eight individuals were found alive. The sample was opened at once and examined for sex-condition. Particulars are given in **1**, p. 1030, lot 113A. Two were functional females, 1 of these being hermaphrodite but full of ripe eggs; the remaining individuals were mostly good males in good condition.

B. Sixteen blacksick oysters sent on from the Fal Estuary beds in July 1925 were treated in the same way as the preceding sample A. When the 7 survivors were examined on July 3, 1926, 1 individual was found to be hermaphrodite with abundant ripe ova. This type of individual is regarded as a functional female. Five others were in good condition as ripe or ripening males and 1 was neuter in poor condition.

Experiment 11. *On Females* (*West Mersea and Fal Estuary*) *Whitesick, July* 1925, *West Mersea, R. Blackwater.*

A. During July 1925, 48 whitesick oysters were found amongst samples dredged at West Mersea, and put in the cage in Deeps on July 21, 1925. When the cage was hauled on July 3, 1926, 41 oysters were found alive and tested July 3–5. None were then found in spawn. On July 7 the whole sample was opened and the sex-condition noted as is given in **1**, p. 1030, lot 113B. Three individuals were found carrying young, 3 were ripe or ripening females, and 1 was a ripe female with sperm in the gonad ; the remainder of the sample were males in various phases except for 3 weakly and neuter individuals.

B. Twenty-one whitesick oysters sent to West Mersea from the Fal Estuary in July 1925 were treated in the same way as the sample A described above. When examined on July 3, 1925, of the surviving 6 oysters 1 was a ripe female ready to spawn, 4 were ripe males in good or very good condition, and 1 was a weakly neuter.

Experiment 12. *On Females Bearing Young* 1926. *Truro Beds, Fal Estuary.*

A. In this experiment 61 Fal Estuary oysters found with black or grey-shelled larvæ in July 1926 were put out in a new cage in Trelissick Reach on July 29, 1926. This sample was hauled and examined on September 29, 1926, to obtain information on gonad changes in the same breeding season as the oysters were found in spawn. The details of this sample are given in **1**, pp. 1031–2, lot 114A, and may be summarised as follows :—

The sample consisted of 43 with normal shells, of which 2 died, and 18 with dumpy shells (for definition see **7**, p. 200), of which 1 died.

TABLE XI.

Category.		Normal. No.	Normal. With relict ova.	Dumpy. No.	Dumpy. With relict ova.
♀ with young		1 Bl.	0	1	0
ripe female		0	0	0	0
♂ phase IV		0	0	0	0
„ V	waning or arrested	2	0	1	0
„ VI		17*	1	11	0
„ VII		9	0	2	0
„ VIII=neuter		10	1	2	0
not observed		2	0	0	0
		41	2	17	0

B. Three whitesick oysters were put out and hauled with sample A noted above. One died ; the two remaining were in male phases IV and V respectively on September 29, 1926, and neither had unspent ova in the gonad (see *loc. cit.*, lot 114B).

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* One of these might have had very young ova, but microscopic sections are required for certainty in identification.

C. A sample of 28 blacksick individuals was also put out in another cage moored to the Poles Rocks, Fal Estuary. These were put out on July 21, 1926, and examined for general gonad condition on September 30, 1926. Three died. The details of the living ones are given in **1**, p. 1032, lot 115A, and may be summarised as follows :—

TABLE XII.

Category.	Normal. No.		Dumpy. No.	
	C.	D	C	D
♀'s with young	2§ (1 sl ; 1 Wh)		0	
ripe females	0		0	
♂ phase IV	1		0	
,, V	2		1	1
,, VI	8§	7§	1	1
,, VII	5*	2	4†	1
,, VIII	1	3‡	0	
	—	—	–	–
Sample C totals	19		6	
Sample D ,,		12		3

D. In the cage moored to Poles Rocks on July 21, 1926, were also isolated 15 oysters found whitesick during July 1926. These all survived and were examined on September 30, 1926. Details of their general condition are given in **1**, p. 1033, lot 115B, and are summarised under D in the table given above.

Experiment 13. *On Females Bearing Young*, 1926, *West Mersea, R. Blackwater.*

In earlier experiments females carrying spawn have been examined after isolation in the sea for twelve months or more, or in the case of the last experiment after about two months. In this experiment 45 blacksick and 66 whitesick oysters were collected and put out in the sea at West Mersea on July 14, 1926, and examined just before the beginning of the breeding season in 1927, namely on May 27, the cage having been hauled on May 26. The details are given in Tables XIV and XV, pp. 39 and 40, and may be summarised as follows :—

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* One with numerous young ova.
† Two with doubtful young ova.
‡ One with doubtful young ova.
§ One with unspent ova, probably many young relict ova in the ♀ with larvæ.

TABLE XIII.

Category.	A. Blacksick, 1926.	B. Whitesick, 1926.
♀'s with young	0	0
ripening and ripe ♀ phases	8	5
young ♀'s	1	1
♂ (♀) B	2	1
neuter	3	0
ripening and ripe ♂'s	21	39
young and developing ♂'s	3	18
died	7	2
	—	—
	45	66

SERIES C. EXPERIMENTS ON RIPE FEMALES AND RIPE FEMALE INTERSEXES.

Experiment 14. *On the Isolation in the Sea of Ripe Females, West Mersea, R. Blackwater*, 1923.

When boring oysters for the purpose of finding males in July 1923, 12 ripe female individuals were discovered. These were returned to the sea in a whelk-pot hung over the stern of a vessel in Thornfleet until October 1923, when they were hauled and opened and examined on October 29. Eight of them were found to have made good shell-growth, of which a photograph is shown in **3**, Fig. 6, p. 379. The sex-phases were as follows :—

TABLE XVI.

Male Phases.	V	VI	VII	VIII
Total 12	2	5	1	4
,, 8 with relict ova	2	1	1	4

All the individuals had spawned, but eight showed indications of a recent female phase in the presence of relict ova in the gonad.

Experiment 15. *On the Isolation in the Sea of Hermaphrodites, West Mersea, R. Blackwater*, 1923.

Four hermaphroditic oysters were found at the same time and in the same way as the females mentioned in Experiment 14. These were also isolated in Thornfleet and examined on October 29, 1923. Three had

TABLE XIV.

Experiment 13, A.

On Females Blacksick, West Mersea, July 1926, *examined May* 27, 1927.

					Sex-elements.			Shell.[3]			
					Sperm-morulæ.			Length in mm.		Shoots in mm.	
o.	Condition of Fish.	Appearance[1] of gonad.	Gonoducts.	Sex-phase.[2]	Ripe.	Unripe.	Ova.	1926	1927	1926	1927
1	f.	sq. & trs. retic.	½ full	ca. ripe ♂	∞	∞	none	74	83	13	0
2.	f.	—	full	ripe ♂	N.O.			60	60	4	0
3.	f.g.	ram. A trs. retic.	empty	♂ IV	∞	∞	none	70	84	13	3
4.	g.	white nf. (♂) ⚥ ♀	filling	♂ (♀) A	few	∞	∞	49	70	22	0
5.	f. to p.[4]	trs. retic. ; st. B	empty	neuter	none	none	none	58	65[3]	13	0
6.	f.[4] [5]	sq. & trs.	do.	♂ V	fair no.	occ.	none	48	56[3]	8	0
7.	v.g.[6]	ram. A op. retic.	do.	♂ (♀) A	v. ∞	f. ∞	f. ∞	57	64	18	0
8.	f.g.	—	full	ripe ♂	N.O.			50	61	10	tr.
9.	f. to p.	—	filling	ca. ripe ♂	N.O.			50	16	15	0
0.	f.g.[6]	ram. A trs. retic. wh.	empty	♂ (♀) A	∞	∞	f. no.	49	64	15	0
1.	g.	—	full ; long	ripe ♂	N.O.			47	63	20	0
2.	g.	—	do.	do.	N.O.			52	61	16	0
3.	g.	—	do.	do.	N.O.			48	48	0	0
4.	g.	—	do.	do.	N.O.			41	55	13	0
5.	g.	—	do.	do.	N.O.			53	62	12	3
6.	g.	sq. & trs. st.	empty	♂ III	few	v. ∞	occ. rel.	55	60	5	4
7.	v.g.	white nf. (♂) ⚥ ♀	filling	♂ (♀) A	∞	few	∞	46	59	12	3
8.	g.	—	full ; long	ripe ♂	N.O.			62	76	20	tr.
9.	f.g.	—	filling	ca. ripe ♂	N.O.			55	63	10	tr.
0.	g.	—	full ; long	ripe ♂	N.O.			65	69	10	0
.	f. to p.[7]	G.D. st. A–ram. A	empty	young ♀ ?	none	none	∞	43	55	16	0
.	g.[4]	sq. & trs., honeyc. & retic.	do.	neuter	none	none	none	52	54	5	tr.
.	v.p.[7]	watery	do.	do.	N.O.			49	56	15	0
.	f.	sq. & trs. honeyc. retic.	do.	♂ I	none	few	none	53	63	10	2
.	f.g.	—	full ; long	ripe ♂	N.O.			54	61	11	0
.	g.	—	do.	do.	N.O.			50	65	15	0
.	f.	—	do.	do.	N.O.			62	78	15	5
.	v.g.	white ff. (♂) ⚥ ♀	full of ova	ripe ♀	occ.	none	∞ ripe	57	65	9	0
.	g.[6]	white nf. (♂) ⚥ ♀	filling	ca. ripe ⚥	v. ∞	none	f. ∞	55	70	15	0
.	f.[6]	sq. & trs. retic. honeyc.	empty	♂ III	few	v. ∞	occ. rel.	47	58	10	0
.	g.[6]	ram. A wh. retic. ♂ ?	empty	♂ (♀) B	∞	∞	f. ∞	67	81	17	0
.	f.g.	—	filling ; long	ca. ripe ♂		N.O.		46	67	22	0
.	v.g.	—	do.	do.		N.O.		54	60	9	0
.	g.[6]	wh. retic. nf. (♂) ⚥ ♀	empty	♂ (♀) B	∞	∞	few	50	73	22	0
.	v.g.	rather sq.	filling ; long	ca. ripe ♂		N.O.		65	66	13	0
.	v.g.	ram. A opaque	empty	♂ (♀) A	v. ∞	none	f. no.	47	59	9	0
.	g.[6]	ram. A wh. & trs. retic.	do.	♂ (♀) A	∞	∞	f. no.	48	70	23	0
.	g.	—	full ; long	ripe ♂		N.O.		58	70	15	0

Notes on Table XIV.

[1] The abbreviations used to denote the naked eye appearance of the gonad will be amplified and discussed in a later communica-on on a seasonal study of an oyster population.

[2] For a description of sex-phases, see **1**, pp. 975 and 981.

[3] The comparison in this sample and that noted in Table XV between the growth of large shell-shoots in the autumn of 1926 and e slight, or absence of such growth in the spring of 1927, is especially interesting (see **3**, p. 377). The length of the shell is measured tero-posteriorly and is on the average about the same as the height measured dorso-ventrally ; the shoot is measured in the mid-ntral line, where it is usually largest, tapering off anteriorly and posteriorly.

[4] Shells chambered indicating constitutional trouble of some kind, at some unknown period.

[5] Muscle spindles (see **5**, p. 48) present in the visceral mass.

[6] An appearance of abundant food reserve material is noted in correlation with the presence of degenerating and/or developing a (see **1**, p. 976).

[7] Mantle cavity choked with mud ; this fact in correlation with the poor condition of the fish indicates permanent weakness.

breviations :

f. = fair or fairly.	g. = good.	v. = very.	p. = poor.	G.D. = Gonad developing.
∞ = numerous.	no. = number.	tr. = trace.		G.L.D. = Gonad little or slightly developed.
				G.M.D. = Gonad mediumly developed.
				G.W.D. = Gonad well developed.

N.O. = not observed, as experience taught that microscopic examination is not necessary in such cases.

neral.

The gills in this sample were mostly coloured slightly green and were thus on the point of the seasonal change from the winter te of being coloured a ferrous-sulphate green to the summer state of white gill. Some gills were brown, i.e. nos. 3, 4, 9, 17, 19, 22, 25, and 38.

TABLE XV.*

EXPERIMENT 13, B.

On Females Whitesick, West Mersea, July 1926, *examined May* 27–28, 1927.

					Sex-elements.			Shell.[3]		
					Sperm-morulæ.			Length in mm.		Shoot in m
No.	Condition of Fish.	Appearance[1] of gonad.	Gonoducts.	Sex-phase.[2]	Ripe.	Unripe.	Ova.	1926	1927	1926
1.	f.g.	f. trs. honeyc. retic.	full ; long	ripe ♂		N.O.		53	80	24
2.	f.g.	do.	do.	do.		N.O.		48	69	18
3.	f.g.	ram. A. trs. retic. G.L.D.	—	♂ I	none	few	none	58	66	10
4.	f.g.	ram. A. wh. & trs. retic. G.M.D.	—	♂ (♀) A	few	v. ∞	f. no.	70	78	10
5.	f.	ram. A. trs. retic .G.L.D.	—	♂ I		N.O.		50	73	16
6.	f.	G.L.D.	full ; long	ripe ♂		N.O.		53	73	10
7.	f.	trs. retic. G.L.D.		♂ I	none	∞	occ. rel.	47	67	19
8.	f.	sl. ram., wh. trs. retic.		♂		N.O.		55	74	18
9.	f.	do.		♂		N.O.		50	80	21
10.	f.	G.L.D.	full ; long	ripe ♂				56	67	17
11.	f.g.	do. sq., & trs. retic.	—	♂ IV	∞	∞	none	57	60	0
12.	v.g.	ram. A. op. G.n.f.D. (♂) ⚥ ♀	—	♂ (♀) A	∞	f. ∞	∞	44	59	13
13.	f.g.		full ; long	ripe ♂		N.O.		38	56	14
14.	f.	trs. retic. G.L.D.	—	♂ I	none	∞ young	none	41	48	7
15.	f.g.	G.M.D.	filling	ca. ripe ♂		N.O.		49	65	11
16.	f.	G.L.D.	do.	do.		N.O.		47	62	13
17.	f.g.	sq. & trs. retic.	—	♂ I		N.O.		63	75	10
18.	f.g.	do.	filling	♂ IV		N.O.		56	68	16
19.	f.	f. trs. G.L.D.	full	ripe ♂		N.O.		49	76	19
20.	g.	sq. & trs. retic.	—	♂		N.O.		55	63	7
21.	g.	do.	—	♂		N.O.		61	63	7
22.	v.g.	ram. A trs. G.W.D.	filling	ca. ripe ♂		N.O.		56	63	8
23.	g.	do	do.	do.		N.O.		63	81	16
24.	v.g.	G.W.D.	do. long	do.		N.O.		56	72	14
25.	f.	G.L.D.	full	ripe ♂		N.O.		46	60	17
26.	g.[6]	ram. A. wh. retic.	—	♂ (♀) B	v. ∞	∞	some	58	66	8
27.	f.	sq. & trs. retic.	—	♂		N.O.		58	68	7
28.	g.	G.M.D.	full	ripe ♂		N.O.		56	61	7
29.	v.g.	G.W.D.	do. long	do.		N.O.		50	69	19
30.	f. to p.	sq. & trs. sl. retic.	—	neuter or ♂ I		N.O.		68	80	9
31.	f.	sq. & trs. sl. retic. G.L.D.	—	♂		N.O.		56	76	17
32.	f.	do.	little in ducts	♂ IV		N.O.		50	58	7
33.	g.	G.M.D.	full	ripe ♂		N.O.		49	60	10
34.	g.[6]	G.v.W.D. white nf. (♂) ⚥ ♀	filling	♂ (♀) A	few	f. ∞	∞	55	65	13
35.	g.	trs. retic. G.W.D.	do.	ca. ripe ♂		N.O.		61	75	16
36.	f.	sq. & trs. retic.	—	♂		N.O.		55	70	20
37.	f.	ram. trs. retic. G.L.D.	filling	♂ IV		N.O.		50	69	10
38.	g.	G.W.D.	full	ripe ♂		N.O.		50	64	20
39.	f.g.	G.M.D.	do. long	do.		N.O.		60	73	11
40.	f.g.	sq. & trs. retic.	filling	♂ IV		N.O.		55	63	6
41.	f.	do.	do.	♂ IV		N.O.		45	62	17
42.	f.g.	sq. & trs. st. B		♂ III	few	∞	none	58	69	12
43.	g.	G.M.D.	full	ripe ♂		N.O.		53	62	13
44.	g.	G.v.W.D.	do. long	do.		N.O.		50	61	12
45.	g.	G.M.D.	do.	do.		N.O.		54	66	16
46.	g.	G.M.D.	filling	ca. ripe ♂		N.O.		58	70	12
47.	f.	G.L.D.	full	ripe ♂		N.O.		45	50	9
48.	f.g.	do.	do.	do.		N.O.		44	51	9
49	f.	st. ram. trs. retic.	little	♂ IV		N.O.		46	53	6
50.	f.	do.	do.	♂ IV		N.O.		53	62	8
51.	v.g.	white (♂) ⚥ ♀ G.F.D.	filling	⚥ (♀)	f. ∞	none	∞ ripe	62	79	13
52.	g.	G.M.D.	do.	ca. ripe ♂		N.O.		63	73	14
53.	f.g.	do.	do.	do.		N.O.		53	68	17
54.	f.	do.	do.	do.		N.O.		50	65	21
55.	g.[6]	ram. A wh. retic. G.M.D.	—	♂ (♀) A	∞	∞	f. ∞	53	63	11
56.	f.g.	sq. & trs. retic. G.L.D.	—	♂ III	rare	∞	none	68	74	10
57.	f.	f. trs. dendritic ducts	filling	ca. ripe ♂		N.O.		45	63	16
58.	f.	st. A—ram. A wh. retic. G.L.D.	—	young ♀	none	none	∞ ripening	64	81	13
59.	f.	G.L.D. ram. retic.	—	♂		N.O.		56	70	17
60.	f. to p.	sq. & trs.	—	♂ V	fair no.	few	none	47	63	16
61.	f.	sq. & trs. st. B	little	♂		N.O.		75	87	6
62.	f.g.	do.	do.	♂		N.O.		62	70	7
63.	f. to p.	trs. retic. G.L.D.	—	♂ I	none	∞ young	none	46	67	21
64.	v.g.	ram. honeyc. G.W.D.	filling	ca. ripe ♂		N.O.		68	73	8

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* See notes to Table XIV for explanatory remarks. In this sample the gills were mostly slightly green : in 11 individuals were brown.

spawned all or nearly all the ova, but 1 had spawned its ova only partially. The latter was in sex-phase VII with relict ova, and with two others, which were in sex-phases VI and VII, had made a perfect recovery from the boring. The fourth had made a very bad recovery from the operation and its gonad had no sex-elements.

Summary and Discussion of Experiments on Isolating Oysters Carrying Young (Series B) and on those with Ripe Eggs (Series C).

The results obtained in the set of experiments with oysters bearing young are summarised in Tables XVII A and B, p. 44, and XVIII, pp. 46–47.

From Table XVII B it is seen that at the end of the same breeding season as that in which the experimental individuals were found, i.e. the 1st summer, a proportion as high as 3·4% were again detected bearing young. In the second summer about 5% were found again with young and an additional 7% were ready to spawn as females. Among the small number of individuals surviving to the third summer of the experiments about 5% were again found with young and at least an additional 15% ready to spawn as females. Among all the experimental oysters about 11% were discovered again in ripe female functioning stages.

It may be presumed that *all* female-functioning oysters revert again to the female phase at some time after passing through an intermediate male (and possibly a neuter) phase. Hence the gross percentage of reversion to the ripe female phase found is small except in the experiment which ran into the third summer. There can be no doubt that the actual reversions occurring were much greater in number than found from the following considerations:—

(1) In several experiments (e.g. 10 and 11) only one test was made during the breeding season, so that only those females existing as such at that time of the season were detectable. It is known that female phases may develop throughout the extent of the breeding season, although on the beds in the River Blackwater a maximum of spawning usually occurs about July.

(2) In some experiments tests were not made until some weeks after the opening of the spawning season, hence early spawners may have extruded larvæ before examination.

(3) In experiments 7, 5, and 4, tests were made only for detecting females with young in the second summer of the experiments. In these cases only those females actually carrying young at the time of examination could be detected.

(4) When tests were made frequently, as in experiments 7, 5, and 4, young-bearing phases may nevertheless have passed undetected in the sea in the intervals of testing.

(5) The presence of ova—recognisable in most cases as relict from a recent spawning—in the gonad of eleven individuals either male or neuter examined in the *second* summer of the experiments, and of two other such individuals amongst the few surviving into the third summer, affords evidence of the occurrence of the undetected production of larvæ among the experimental oysters.

Thus the reversions found by experiment in all cases can certainly be regarded as smaller than actual.

On the oyster beds it may reasonably be expected that the reversions to the young-bearing stage would be greater than those actually occurring under experimental conditions, the detrimental effect of which is demonstrated by the known heavy mortality. The attainment of the functional female phase may be postulated to be dependent upon a period of anabolic metabolism, and the building up of good reserves would undoubtedly be delayed or depressed by those detrimental conditions ancillary to the experiments already referred to on p. 26. Thus reversion to the female phase on the oyster grounds may reasonably be expected to be not only greater than that found in the experiments, but also greater than that actually occurring in them.

Although a greater percentage of reversions to the young-bearing phase may occur naturally on the beds than in the experiments, there are indications that a small proportion of the spawning taking place under experimental conditions may be a result of these conditions. It is clear that a correct estimation of any error introduced by the conditions of the experiment is of the greatest importance in assessing the results.

During the course of these experiments the importance of incomplete spawning in females has become gradually recognised. A discussion on the fate of unspawned ova is given in **1**, p. 974, and **6**, where it is regarded as probable that in a few cases out of the large number of observations made a given female may as a result of incomplete spawning in the first instance have spawned successfully a second time in one season from one batch of ova matured for the first spawning.

Experiment 12 was designed to obtain information on this matter. It was found that among 98 surviving oysters examined in September 1926 (see Table XVII), 4 were carrying young, although all had been found previously in July with either embryos or larvæ. The condition of the young in two of these four cases indicated that spawning had occurred recently; it is possible, but not probable (owing to the small size of the larvæ), that in the two others the larvæ may have been retained in the mantle cavity from July. In Experiment 5, when 10 individuals were examined five weeks after detection with young, 1 had larvæ which had in all probability been retained during the five weeks. Thus retention of larvæ and incomplete spawning may give an appearance of the assumption of a second female phase in one and the same breeding season. Whether unspawned ova can be successfully spawned after remaining in the gonad during the winter is a moot point, though improbable. Eggs remaining in the gonad at the approach of winter are *usually* evacuated or begin to degenerate *in situ* in the gonad. Relict eggs may, however, contribute to hastening the next female phase by adding to the food reserves in the body by their absorption.

Apart from this, it may be considered that female spawning in the second summer due to incomplete egg-spawning in the previous summer is a rare event, if indeed it occurs at all. An individual which retains ova in the winter is usually of the type designated as " curdley " (see **1**, Tables IV and IX).

In **1**, Table IV, p. 999, a record is made of the occurrence or absence of unspawned ova in about 700 recently spawning females. On analysis (see **6**) it is found that about 54% retain few or more eggs after spawning ; 43% of these containing a few scattered eggs, while 11% may have many in scattered or large patches. Among this large sample as many as 22 individuals are recorded with the gonad from $\frac{1}{3}$ to $\frac{7}{8}$ spent. If it were possible for these individuals to spawn successfully again in the same season the percentage would attain the figure 3, very nearly that found in Experiments 12, 7 and 5, namely 3·4. (See Tables XVII A and B.)

Thus the oysters bearing young again in September in Experiment 12 must be regarded as having almost certainly spawned a second time from eggs matured earlier in the season ; it is also possible that others undergoing such a second spawning may have occurred undetected during the course of this experiment.

Among the experiments where the samples were opened in the second summer, the results obtained in Experiment 11A are especially interesting (see Table XVIII, sample 18). In this case there was little mortality during the winter, 41 surviving out of 48. Correlated with these beneficent conditions is the occurrence of 3 oysters with young and 4 ripe female phases in the following July, a total of about 17% mature female-functioning reversions. In this set of experiments 11·7% of reversions occurred. Twenty per cent of reversion is also shown in Experiment 5, where the mortality in the preceding winter was low. Even if 5% of these be attributed to the influence of incomplete spawning in the preceding breeding season, there is still a significant margin left to prove reversion in the second summer, especially when it is remembered that the figure obtained is a minimum in comparison with that likely to occur in wholly natural animals.

In the small number of individuals surviving into the third summer, as in Experiment 4, one quarter of the sample were in mature female phases at the time of examination.

CONCLUSIONS FROM EXPERIMENTS ON OYSTERS WITH YOUNG.

The experiments therefore prove that oysters which have borne young in one summer do attain a new female phase and bear young again in significant (but small) numbers in the next summer; a rather larger proportion attained new female phases two years later. There is good reason to believe that the percentage of reversion to female phases will be very much higher in wholly natural than in the experimental oysters, and that more reversions occurred in the experimental oysters than were discovered.

TABLE XVII A.

SUMMARY OF EXPERIMENTS ON ISOLATING OYSTERS WITH YOUNG.

		1st Summer.			2nd Summer.				3rd Summer.			
No. of Expt.		No. of oysters.	No. of tests.	No. of ♀'s with young.	No. of survivors.	No. of tests.	No. of ripe ♀'s and ⚥.	No. of ♀'s with young.	No. of survivors.	No. of tests.	No. of ripe ♀'s. and ⚥.	No. of ♀'s with young.
12	A	82 (56)*	*1*	**2** :								
	B	3 (2)	*1*	0 :								
	C	28 (25)	*1*	**2** :								
	D	15 (15)	*1*	0 :								
13	A	45	–	–	38	–	8+2	– :				
	B	66	–	–	64	–	5+1	– :				
8		60	–	–	38	*2*	1	**4** :				
9		75	–	–	48	*2*	0	**2** :				
10	A	38	–	–	28	*1*	2	0 :				
	B	16	–	–	7	*1*	1	0 :				
11	A	48	–	–	41	*1*	4	**3** :				
	B	21	–	–	6	*1*	1	0 :				
6		29	–	–	20	*2*	1	**2+1**?				
7		21 (21)	*1*	0	19–3†	*4*	–	**4**	1 died			
5		27 (27)	*1*	**1**	5–1†	*4*	–	0	2 died			
4		78	–	–	32–4†	*3*	–	**1**	19 (3 died)	*3*	3+1	**1**
	Totals	146		**5**	346		23+3‡	**16+1**?	19		3+1§	**1**

TABLE XVII B.

	No. of oysters tested.	No. of functioning. ripe ♀'s	No. of ♀'s with young.	Total functioning ♀.	Total % functioning ♀.
1st Summer	146‖	—	5	5	3·4
2nd do.	346¶	23(+3)**	16(+1?)	39(+4)	11·3 to 12·4
3rd do.	19	3(+1)	1	4(+1)	21·0 to 26·3
Totals	511	26(+4)	22(+1?)	48(+5)	10·8 to 11·9
	67‖¶				
	444				

---

* The numbers in brackets in Table XVII A give those surviving to be tested in the first summer.

† Died during the second summer. ‡ Intersexes with ova nearly ripe.

§ With numerous doubtfully healthy ova.

‖ Includes 48 from Experiments 7 and 5 carried forward or died at end of first summer.

¶ Includes 19 from Experiment 4 carried forward at end of second summer.

** The figures bracketed in Table XVII B are derived from the totals given in Table XVII A.

SEX-PHASES INTERVENING BETWEEN SUCCESSIVE FEMALE PHASES.

It has been shown (**1**, Table IV) that among 702 oysters carrying young 97% of such individuals *immediately* pass into an active male phase after the act of egg-spawning. Many hundreds of similar cases have since been recorded. Additional evidence is afforded by the sex-phases recorded in Table XVIII from the B series of experiments. Thus, there can remain no doubt that the translation from a female to an active male phase occurs normally in *O. edulis* after the egg-spawning act. The small percentage of abnormalities—which consisted mostly of no assumption of the male phase—occurred at the end of the breeding season, when the gonad is passing into a passive condition. This fact is quickly seen from a glance at Table XVIII, pp. 46–47. Among individuals examined in July (Sections 1, 4, and 6) the male-phases are predominant, and are mainly IV, V, and VI, indicating that the gonads are still producing spermmorulæ. On the other hand samples examined in September (Section 2) contain a high proportion of waning and neuter phases (e.g. VI, VII, and VIII). At the beginning of the second summer male phases still occur in high proportion. but are predominantly active, and it is interesting to note contain some quite young phases, namely I to III. It is thus shown that at the end of the breeding season sperm-production wanes or ceases but becomes active again in a high proportion of comparable individuals (80%) in the following early summer. During the early summer a proportion of individuals varying in the experimental material from 10% to 15% pass over into a functional female phase. A comparison of the totals in Sections 2 and 3 in the Table gives the suggestion that a proportion of the neuter individuals in September become female in the following spring. Further evidence is required, however, before this sequence can be acclaimed as a fact. No data are available from these experiments for discovering what proportion of individuals would pass from 2nd summer male phases into a 2nd summer female phase, but it is hoped to obtain the required information from an intensive study of seasonal changes in sex-phases in an oyster population. Such a study was made in 1926–27, and the results are being worked out.

In the 3rd summer the female phase was assumed in a larger proportion of the experimental oysters; 50% in Series A (see Table IV, p. 27) and 21% to 26% in Series B (see Table XVII B, p. 44), *excluding* the individuals showing signs of having recently passed through the female phase by the presence of recently relict ova in the gonad. Under wholly natural conditions there can be little doubt that the percentage of these transitions to the female phase would be much higher than in the experimental. The experiments nevertheless afford a valuable basis for more enlightening field studies. For example, it is relevant to record that in

TABLE

SEX-PHASES OF O. EDULIS, *occurring in samples examined at*

(Data derived from material

No. of Section.	Sample.	Site of Expt.	No. of Expt.	Expt. begun.	No. isolated and condition of young. Bl.	Wh.	Mixed.	Origin of oysters.	Month of examination.	No. surviving to be tested or examined.
1.	Sex-phases found five weeks later (July). (In the same breeding season.)									
	1	R.Y.	5a	June			10	various	July	**10**
2.	Sex-phases found two to three months later in the 1st summer (Sept.–Oct.), (within									
	2	Fal R.	12A	July	63			F.E.	Sept.	39
	3	do.		do.	18			do.	do.	17
	4	do.	12B	do.		3		do.	do.	2
	5	Fal E.	12C	do.	22			do.	do.	19
	6	do.		do.	6			do.	do.	6
	7	do.	12D	do.		12		do.	do.	12
	8	do.		do.		3		do.	do.	3
	9	W.M.	6a	do.			2	W.M.	Oct.	2
	10	do.	14	do.			12*♀	do.	do.	12
	11	do.	15	do.			4†⚥	do.	do	4
							Totals of Section 2			**116**
3.	Sex-phases found at the approach of the next breeding season (2nd summer; May).									
	12	W.M.	13A	July	45			W.M.	May	38
	13	do.	13B			66		do.	do.	64
							Totals of Section 3			**102**
4.	Sex-phases found during the next breeding season (2nd summer; July).									
	14	W.M.	8	July	60			W.M.	July	38
	15	do.	9	June		75		do.	do.	48
	16	do.	10A	July	38			do.	do.	28
	17	do.	10B	do.	16			F.E.	do.	7
	18	do.	11A	do.		48		W.M.	do.	41
	19	do.	11B	do.		21		F.E.	do.	6
	20	do.	6	Aug.			29	W.M.	do.	20
							Totals of Section 4			**188**
5.	Tested only for young-bearing in the next breeding season (2nd summer; ca. July).									
	21	W.M.	4	July			78	W.M.	July	32–4
	22	R.Y.	5	June			27	various	do.	5–1
	23	R.Y.	7	June–Aug.			21	do.	June–Aug.	19–3
							Totals of Section 5			**56**
6.	Sex-phases found two years later (3rd summer; July).									
	24	W.M.	4c	—			(78)	W.M.	June–July	**16**
			Sum Totals		**268**	**228**	**261**			*488*
			Adjustments				78‖			44‡
			Adjusted Totals		**679**					**444**

* 12 found as ripe female by boring the shell.

† 4 found as ripe ⚥ by boring the shell.

‡ Comprises some samples not shown in Table XVII (i.e.

1. 2. 3. The small figures give the number of individuals in the

ϕ The numbers in brackets are included in one or other of the

‖ 78 individuals used for Sample 21, Experiment 4, are recorded

XVIII.

various intervals of time after being detected with young.

isolated in cages in the sea).

Male phases.							Neuter.	Female phases.						No. of	
										Ripe phases.					
I	II	III	IV	V	VI	VII	VIII	♂(♀) B	Juv. ϕ Dev.	♂(♀) A	☿	♀	♀ with young.	Sample.	Section.
–	–	–	**3**	**3**	**3**	–	–	–	–	–	–	–	**1**	1	**1.**
but at the end of one and the same breeding season).															**2.**
–	–	–	–	2	17^1	9	10^1	–	(1?)	–	–	–	1	2	
–	–	–	–	1	11	2	2	–	–	–	–	–	1	3	
–	–	–	1	1	–	–	–	–	–	–	–	–	–	4	
–	–	–	1	2	8^1	5^1	1	–	(1)	–	–	–	2	5	
–	–	–	–	1	1	4^2	–	–	(2?)	–	–	–	–	6	
–	–	–	–	–	7^1	2	3^1	–	(1?)	–	–	–	–	7	
–	–	–	–	1	1	1	–	–	–	–	–	–	–	8	
–	–	–	–	–	1	–	1	–	–	–	–	–	–	9	
–	–	–	–	2^2	5^1	1^1	4^4	–	–	–	–	–	–	10	
–	–	–	–	–	1	2^2	1	–	–	–	–	–	–	11	
–	–	–	**2**	**10**	**52**	**26**	**22**	–	**(1 + 4?)**	–	–	–	**4**		
1	–	2	–	21	–	–	3	2	1	6	1	1	–	12	**3.**
	18			39		–	–	1	1	4	1	–	–	13	
	21			**60**			**3**	**3**	**2**	**10**	**2**	**1**	**0**		
–	–	–	12	10	8^1	3		–	–	–	–	1	4	14	**4.**
–	–	–	3	13	21^2	3^1	5^3	–	–	–	–	–	3	15	
–	–	–		24		–	2	–	–	–	1	1	–	16	
–	–	–		5		–	1	–	–	–	1	–	–	17	
–	–	–		31^1		–	3	–	–	–	1	3	3	18	
–	–	–		4		–	1	–	–	–	–	1	–	19	
–	–	–	7	4^2	3^1	–	2	–	–	–	–	1	2 + 1?	20	
				145		**6**	**14**				**3**	**7**	**12 + 1?**		
													1	21	**5.**
													0	22	
													4	23	
													5		
–	–	–	**6**	**2**	–	–	$\mathbf{3^2}$	**1**	–	**1**	**1**	**1**	**1**	24	**6.**
								4			*26*		*22 + 1?*		

samples 1, 9, 10, 11) and sample 24 counted twice.
respective phases with either small patches of unspent or—rarely—developing ova in the gonad.
male phases and are not to be counted in the sample total.
again in Sample 24, Experiment 4 c.

three successive seasons on the Fal Estuary beds (Truro Rights) about 50% of the oyster population have been found to be ripe as functional females at about the beginning of each breeding season (see also **7**, p. 27). These facts alone show that on these beds there is on the average a reversion to the female phase at least every other summer.

A comparison of the male phases of the oysters in the experiments of Series A (see Table IV A, p. 27) with the male phases of individuals which were females in the preceding summer (see Table XVIII, Section 4, pp. 46–47) brings out a close similarity. Hence the males used in the Series A may have been mostly female in the summer before that in which they were identified. Some of these might very well have been female two summers ago, and therefore the rapid change to female observed in one instance (see p. 24) is—in the light of the results of these experiments and if the individual were normal—not outside expectation.

The young female stage was observed in two individuals in Experiment 13 when the whole sample was opened at the approach of the breeding season in May.* Seasonal studies have proved that the bulk of the females in an oyster population develop rapidly in the spring and early summer, hence examinations made about April -July would be the most favourable for discovering young females on most English beds. The relatively small proportion of all the different types of female phases found *in the experiments* is important in indicating :—

(1) that there is no *automatic* return to the female phase in the 2nd or the 3rd summer after that (counted as the 1st summer) in which young are borne.

(2) A return to the female phase may occur in the following breeding season (2nd summer) in a small but significant proportion of individuals.

(3) A higher proportion may revert to the female phase in the 3rd than in the 2nd summer.

(4) The male phase following egg-spawning may persist throughout the 2nd summer and possibly in the 3rd summer.

It is emphasized that these are *experimental* results, and that there is virtual certainty that the sexual processes follow each other more rapidly and more regularly on the oyster grounds than is apparent from these experiments.

Intersexes, or various hermaphrodite conditions, occur in most of the experimental samples which were examined after the 1st summer, and are especially abundant in Experiments 12 and 13 (see Section 3, Table XVIII). This result in a sample examined in May is in accordance with the findings from seasonal studies, in which it has been proved (unpublished) that the female phase may be assumed very rapidly and superimposed upon a variety of the male phases.

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* Great caution is required in assessing young ova in recently-spawned individuals; in these cases young ova are not infrequently retained in the gonad (see Section 2, Table XVIII).

Thus the experiments show that after an oyster has spawned as a female a sperm-producing phase is assumed automatically (with rare exceptions at the end of the breeding season). Sperm-production is active for about one month and then wanes. At the approach of autumn when food-reserves are usually being accumulated, the gonad assumes a quiescent condition in a large proportion of individuals, but in some remains still active. In the first winter the gonad remains apparently in either a neuter condition or in arrested and mostly late male phases. In the following spring a new phase of male activity may begin, or the arrested male phase be continued. In some cases an active female phase is superimposed upon neuter individuals to give pure females, or upon a variety of male phases to give various types of hermaphrodites. These intersexes with ripe newly formed ova are with little doubt mostly, if not all, female-functioning, but are not all definitely proved to be of this nature by the experiments herein described (see p. 19 (c), and Experiment 15, p. 38); the rarity of purity found (unpublished researches) amongst apparently pure ripe females enhances the probability that these types of intersex produce larvæ.

DISCUSSION AND CONCLUSIONS.

The experiments herein described prove definitely for the first time that male individuals of *O. edulis* pass into the female condition *in significant proportion* within twelve months and that greater proportions attain the female condition in two years. The experimental conditions render it probable :—

(1) that only a proportion of the actual change over to the egg-producing stage in the experimental material has been observed, and

(2) that the actual changes in the experiments into female phases are less than would occur naturally when the molluscs lie free on the grounds.

For these reasons it is considered advisable to obtain further information on the rate and proportion of the change from the male to the female phase from studies in seasonal changes in sex-condition throughout an oyster population. Data for such a study have already been obtained, and will be discussed in the near future.

It would appear to emerge from the experiments—in accordance with expectation—that the change from male to female is not automatic as is the change from female to male. The age of the experimental oysters was not known definitely, although it could be stated with certainty that the bulk of the individuals ranged between 4 and 6 years. It is conceivable that the period elapsing between successive female phases may vary with age, but the fact that *O. edulis* may under *optimum* conditions become female at an age of one year (**8**) on English oyster beds indicates that age is not an all-important factor. The predominant factor in the change from the male to the female phase would seem to be the experience of a period of anabolic metabolism ; for this, abundant food and healthy conditions in general are required. In some of the experiments these conditions were certainly not fulfilled during the whole period of the experiments.

The small proportion of reversions to the female phase in about twelve months and the larger proportion after two years indicates that the normal period intervening between successive female phases may be two years on English beds. Many of the experiments were not, however, designed to run for two years, and in those maintained for that period the conditions (e.g. continual testing) were admittedly bad. In new experiments in the future it would be advisable to leave some of the experimental oysters in the sea undisturbed, except for cleaning, for two years, in order to maintain the best possible conditions for determining the percentage of reversion to the female phase for this period of time.

SUMMARY.

Under such environmental conditions as occur on English oyster grounds, it has been found by the use of experimental cages that oysters proved to be male in a given breeding season change to functional females in significant numbers (a minimum of 10% to 16%) in the next breeding season : among a small number of survivors 50% became functional females within about two years.

Experiments on isolating in the sea oysters which have been found with young prove also that a significant number of individuals (ca. 11%) revert to mature female phases within about twelve months ; in experiments extending over two years a higher proportion (a minimum of 21%) among a small number of survivors reverted to mature female phases under conditions which are known to have been and were necessarily unfavourable.

Owing to experimental difficulties, which are discussed, it is considered highly probable that the proportion of changes or reversions to the female phase detected is smaller than that actually occurring in the experiments and evidence is advanced that it is much smaller than occurs when the oysters are lying free and undisturbed on the oyster-bed.

On the other hand it is also shown that a small proportion of individuals

(about 3%) may spawn twice in *one* breeding season from one batch of eggs if a high degree of incomplete spawning occurs at the first attempt. The bearing of this phenomenon on the experimental results is discussed.

The experiments indicate that two years may be the more usual period intervening between successive normal female phases on English oyster beds, but new experiments conducted on different lines are required to obtain further direct information on this problem. This result is in harmony with statistical investigations, which show that females revert to the female phase at least every other breeding season.

The sex-phases found by experiment to intervene between successive female phases are recorded and discussed.

While providing important facts it is regarded that the experiments are inadequate to give a representation of the natural phenomena, and that a clearer picture of the natural changes is more likely to be obtained from a comprehensive population study, for which the experimental results herein described will provide a solid basis.

On Experiments with Oysters in Cages.

It is an interesting and somewhat surprising fact that the isolation of oysters in a cage on the natural oyster bed introduces in itself an important modification of the natural habitat. In the cages utilised in the later experiments herein described a large mesh ($1\frac{1}{2}$ inches in diameter) was utilised, as it was soon realised that the $\frac{3}{8}$-inch mesh of the cage used at West Mersea too readily permitted an accumulation of mud. There are, however, limits to the size of mesh which can be used with safety, for any of the bivalves may slip or project partially through a mesh and in that way be prevented from opening or growing shell-shoots properly. The mesh prevents so free a flow of water over the isolated oysters as occurs on the neighbouring ground. As a consequence an accumulation of silt occurs in the cage, especially if large numbers of the larger simple Ascidians, e.g. Ciona, *Ascidiella aspersa* and *Ascidia conchilega* settle on the oysters or cage and grow; their excreta add to the accumulation of silt in the cage. Silt settling in this way may either choke the oysters or interfere very seriously with normal nutrition by necessitating a large intake of silt in feeding with the consequent loss of energy in voiding it. To obviate some of these disadvantages the cage was raised off the bottom on a table structure; this arrangement gave better results than a cage lying directly on the bed. The disadvantages of a table-cage are that it is more difficult to put out and is more easily upset while lying at the bottom. On a commercial bed it is inadvisable to buoy a cage since the buoy-ropes may inadvertently be fouled by ships passing in the dark.

To prevent the accumulations of growth and silt in the cage it is advisable to raise it as frequently as possible. With a table-cage moored on the bottom frequent cleansing in this way is a laborious and expensive process, unless the experimenter be working continuously near the site of the experiment. A cage lying directly on the bottom can be relatively easily raised and cleaned on frequent occasions. Attachment of the anchors to the legless cage can be made upon the strong iron framework around which the iron mesh-work is secured. Pairs of handles along each edge of the cage at the top as well as the bottom were found extremely useful for one or other of the operations.

It is important to have the cage constructed so that every compartment can be recognised without a label, and the provision of iron-wire mesh shelves in each compartment is an additional advantage for isolating special oysters of different classes easily and quickly. If a permanent shelf be provided it is easy to construct a cover to make a new cagelet within any compartment. In a later design permanent but short legs were obtained by simply allowing the strong vertical corner rods of the framework to project beyond the bottom of the cage. A design of this kind is useful in certain kinds of experiments, though the legs may require strengthening in other ways if much weight is carried. In making the centrally placed lid regard must be paid to the accessibility of the recesses of the different compartments, but the safety accruing from the central lid is a compensation for a little trouble in handling the experimental material.

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Chemical Constituents of Biological Importance in the English Channel. Part III. June–December, 1932. Phosphate, Silicate, Nitrate, Hydrogen Ion Concentration, with a Comparison with Wind Records.

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With 3 Figures in the Text.

When considering wind records, the Beaufort number, B, may with advantage be replaced by its cube, B^3. According to the Observer's Handbook of the Meteorological Office (1921), this is a measure of wind force :—

$P=0{\cdot}0105B^3$, where

P=Force in lb., registered by a circular disc one square foot in area facing the wind as in the plate anemometer when the density of the air is normal, and

B=Beaufort number.

The relation between B and B^3 is :—

B	1	2	3	4	5	6	7	8	9
B^3	1	8	27	64	125	216	343	512	729

At Mount Batten Air Station, Plymouth, wind records are made three times daily. These values have been cubed and the mean taken as the daily, mean cube Beaufort number, to give a mean value of the amount of wind disturbance each day. They are plotted for three periods in Fig. 1. The directions *from* which the wind blew are shown by arrows on the graph. The mean cube Beaufort number may afford a more useful index of the capacity of the wind to cause mixing and turbulence in the sea than the Beaufort number itself.

The conditions found on August 16th, 1932, were directly related with the wind in the preceding month (Figs. 1B and 2). On June 16th and July 13th, at E1, the thermocline was found at 25 metres, above which the temperature gradients were practically uniform. But on July 27th, 28th, and 29th, mean cube Beaufort numbers, 165, 105, and 115 were registered. These winds mixed the water thoroughly down to 10 metres, to give a uniform temperature of about 17·4°–17·5°. Subsequently with quiet sunny weather, the surface layers warmed to about 18·7°. The layer between 10 and 20 metres, sandwiched between two thermoclines, was of exceptional stability and its chemical composition was very unusual.

Conditions in August, 1931, were very different (Fig. 1A). The ten days prior to August 26th, when a cruise was made, showed intermittent strong winds reaching up to a mean cube Beaufort number, 320, on the 20th. These caused very marked vertical mixing right to the bottom by

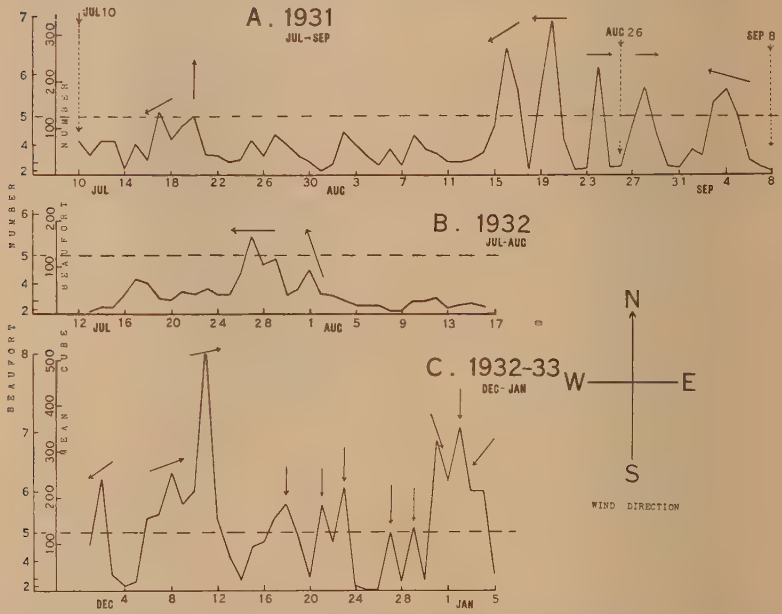

Fig. 1.—Daily Mean Cube Beaufort Numbers (Plymouth, Mount Batten). A. Between cruises on July 10th, August 26th, and September 8th, 1931, including stormy weather at end of period. B. Between cruises on July 13th and August 16th, 1932. C. December 1st, 1932, to January 5th, 1933. In each case a horizontal pecked line is drawn at mean cube Beaufort number, 125, equivalent to Beaufort number, 5. In each stormy period the direction *from* which the wind blew is shown by arrows.

the 26th, although complete uniformity was not attained until some days later (Part I, p. 681).

Thus in July, 1932, three days of wind with mean cube Beaufort numbers around 125 were able to break down the stable layering down to 10 metres, but had little effect further down. In August, 1931, strong winds, around B^3, 200–300, acting for a longer period, were able to break down the thermocline completely. The mean cube Beaufort number brings out this factor much more clearly than the Beaufort number itself.

THE DISTRIBUTION OF NUTRIENT SALTS ON AUGUST 16TH, 1932.

The effect of the stratification of the water in mid-August on the distribution of silicate, nitrite, and pH is shown in Fig. 3, in which the scale relative to depth is the same as in Figs. 2, 3, and 5 in Part I and Fig. 1 in Part II.

High concentrations of silicate were found in the stable intermediate layer (Table I); 270 and 300 mg. SiO_2 per cubic metre were found at 15 and 20 metres respectively, compared with 110 mg. at 10 metres and 175 mg. at 25 metres. Between 10 and 20 metres there was a difference in density, σ_t, of 1·15 units, so that it would seem that dead diatoms were trapped on the thermocline and their skeletons re-dissolved. This occurrence thus provides yet further evidence for the rapid re-solution of silica in the summer months, suggested in Part I, p. 695. On August 16th, 1932, the average silicate content of the water column was 190 mg. per cubic metre. This fell, to give the usual September minimum, on September 12th (120 mg.), followed by a rise to 180 mg. on October 4th.

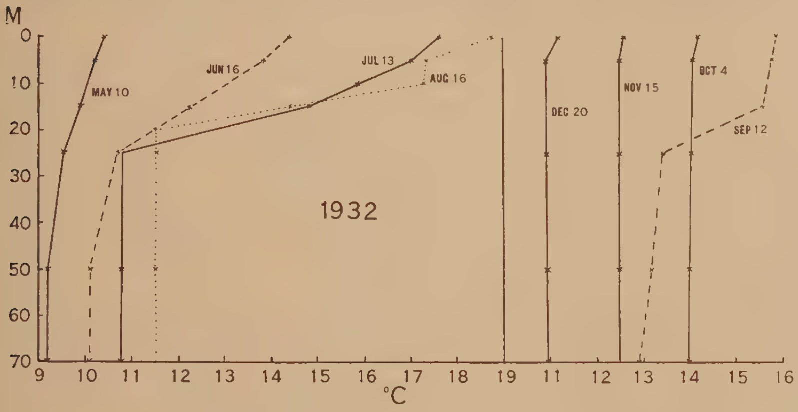

FIG. 2.—Temperature (°C.) at Station E1, Summer and Autumn, 1932.

On August 16th also, extremely high values for pH were found at E1 at 15 metres. There can be no doubt as to the accuracy of these figures since they were found with cresol red, xylenol blue, and thymol blue, in each case with duplicate samples from different bottles. It should be stated that the samples had not been preserved since determinations of pH were not part of the programme. The determinations were made just twenty-four hours after collection with the buffers used in the previous year's work. These were still in good condition. Any error due to bacterial action in the samples or to absorption of carbon dioxide from the atmosphere would tend towards low values for pH and not high ones.

TABLE I.

Station E1.

Depth in metres.	Phosphate. P_2O_5, mg./m³. 1932 15/6	16/8	12/9	27/10	15/11	20/12	Silicate.‡ SiO_2, mg./m³. 15/6	13/7	16/8	12/9	4/10	15/11	Nitrite. N, mg./m³. 16/8	12/9	27/10	15/11
0	13	0	0*	24*	21*	22*	75	98*	175†	230	210	175	1·0	0·32	13·5	4·32
5	1	0	4	–	22	23	55	55	100	105	200*	180	0·0	0·20	–	4·27
10	–	–	–	–	–	–	–	60	110	–	–	–	0·0	–	–	–
15	5	0	5	–	–	–	75	110	270*	105	–	–	0·0	0·58	–	–
20	–	–	–	–	–	–	–	–	300	–	–	–	2·1	–	–	–
25	5	3	11·5*	–	22	25	65	110	175	105	160	–	1·1	14·6	–	4·27
50	–	2	11·5	–	21	27	80	140	190	140	190	190	2·2	19·5	–	4·11
68–70	13	–	15	–	20	30*	70	120	220	105	170*	150*	3·0	25·0	–	4·00
A	16/6	18/8	14/9	29/10	17/11	21/12	17/6	14/7	17/8	13/9	6/10	16/11	17/8	13/9	29/10	16/11

Station E1.
Carbon Dioxide System on August 16th, 1932.

Depth in metres.	pH_w	$pH_{12°}$	pCO_2§ (Atm. × 10^{-4})	ΣCO_2§ (c.c./l.).
0	8·24	8·30	2·3	43·9
5	8·29	8·35	2·0	42·9
10	8·30	8·36	1·9	42·8
15	8·45	8·48	1·2	41·0
20	8·27	8·27	2·1	44·6
25	8·27	8·27	2·1	44·6
50	8·27	8·27	2·1	44·6
69	8·27	8·27	2·1	44·6

Station E2.

Depth in metres.	P_2O_5 1932 15/11	SiO_2 13/7	15/11	Nitrite-N. 15/11
0	26	110*	135	2·04
5	26	75	110	1·95
10	–	75	–	–
15	–	175	–	–
25	27	175	140	1·98
50	27	155	140	1·96
75	27	–	–	1·95
87 or 91	26	155	110	2·13

L Surface Stations
Nitrite—N.

Station.	mg./m³. 1932 12/9	15/11
L1	6·7	10·0
L2	4·25	9·8
L3	3·65	10·6
L4	1·86	13·3
L5	1·44	11·8
L6	0·42	12·2
E1	0·32	4·32
Mid E1–E2	–	4·08
E2	–	2·04

A. Date of analysis.
* Mean of duplicate analyses.
† Sample very cloudy. Reading after standing one hour in comparison tube; approximate only.
‡ Samples from waxed bottles.
§ Derived from pH, temperature and salinity.

The 20-metre samples were indistinguishable from those drawn from 25, 50, and 69 metres (bottom).

The partial pressure and total volume of carbon dioxide, found from pH, salinity and temperature, by means of the tables of Buch *et al.* (1932), are given in Table I. The partial pressure at 15 metres was about half that at the surface. It would seem that photosynthesis was proceeding in the 15-metre layer which was not mixing with the layers above and below it. In this layer phosphate was undetectable and only 5 mg. P_2O_5 per cubic metre had been found a month previously. It is quite probable that the intense regeneration of silicate was accompanied by simultaneous phosphate formation and that this never accumulated sufficiently to become detectable, being used up as it was formed. A similar consumption of carbon dioxide during a period when nutrient salts appeared scarce was noted in Part II (p. 738), a rapid fall in carbon dioxide occurring in June, 1931, when nutrient salts remained very low. This was especially the case above the thermocline.

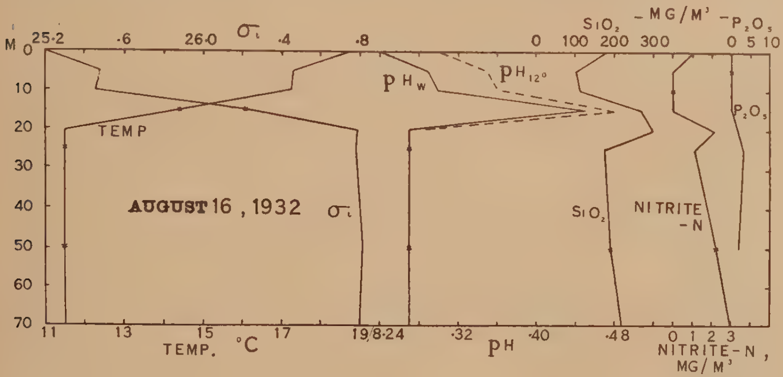

FIG. 3.—Conditions at Station E1 on August 16th, 1932. Temperature (°C.); density (σ_t); pH_W and $pH_{12}°$; SiO_2, nitrite-nitrogen and P_2O_5 (each mg./m³).

Nitrite also showed a somewhat irregular distribution between the thermoclines on August 16th. By September the very stable stratification had begun to break down although a marked thermocline remained at 15–25 metres, above which the amount of nitrite was small. Beneath it conditions were similar to those found there by Atkins (1930) in August and September, 1928. The maximum amount (25·0 mg. N per cubic metre) was found at the bottom, suggesting that nitrification was then most active there.

On October 27th, the surface figure (13·5 mg. N per cubic metre) was probably typical of the whole water column and lies close to the figures found on October 2nd, 1928 (13·3 mg.), and October 20th, 1931 (11·5 mg.).

Later the amount of nitrite at E1 fell away, again in agreement with former years. But in or about December in each of the four years for which data are available, the inshore water has shown a notably higher nitrite content than the water at E1 (Table II). In 1930 and 1931, no clear relation could be seen between the distribution of ammonia and nitrite. The cause of these high, mid-winter, inshore nitrite figures is not very evident.

TABLE II.

EARLY WINTER VALUES FOR SURFACE NITRITE-NITROGEN (MG./M^3) FOR FOUR DIFFERENT YEARS.

Station	30/11/28	2/1/29	11/11/30	4/12/30	13/1/31	30/11/31	31/12/31	15/11/32
L1	6·0	9·5	—	—	—	10·1	5·3	10·0
L2	3·9	9·5	—	—	—	10·9	5·0	9·8
L3	3·3	9·2	—	—	—	11·8	4·7	10·6
L4	3·3	7·7	13·5	5·8	8·2	12·0	2·6	13·3
L5	—	5·6	—	—	—	13·9	1·6	11·8
L6	1·3	3·5	—	—	—	2·5	1·1	12·2
E1	1·4	3·1	2·1	2·05	0·37	0·87	1·13	4·32
Mid E1–E2	—	—	—	—	—	$\leq$1·5	—	4·08
E2	—	—	—	—	—	0·54	—	2·04

It should be remembered that, when seasonal changes of nutrient salts in the English Channel are under consideration, exactly the same body of water cannot be examined on each cruise, so that it is not permissible to treat of events as occurring in a completely closed cycle (cf. Part I, pp. 678, § 3, and 708, § 4).

MIDWINTER PLANKTON OUTBURSTS, SUNSHINE AND WIND.

A "normal" figure for the daily mean cube Beaufort number, B^3, in December, calculated from the records for the nine years, 1924–32, is 102, equivalent to a "normal" Beaufort number of 4·7.

In 1925, between the cruises of November 11th and December 11th, phosphate at E1 fell by 13 mg. P_2O_5 per cubic metre at the surface, by 7 mg. at 10 metres, and by 6·5 mg. as an average of the whole column. For the ten days preceding the cruise of December 11th, sunshine averaged 3·6 hours a day (the normal for Plymouth for December is 1·58 hours) and the average value of B^3 was 55 (B=3·8). The weather was thus favourable to a surface outbreak.

In 1926, between the cruises of December 13th and 31st, phosphate fell by 5 mg. P_2O_5 (surface), 7 mg. (5 metres), and 7 mg. (average content). For the sixteen days preceding the 31st, sunshine averaged 3·2 hours and B^3 averaged 80 (B=4·3). On December 23rd, 24th, and 25th, the values of B^3 were 165, 125, and 165, thus putting up the average. During most of the period conditions were favourable to a surface outbreak. The strong northerly winds at Christmas account for the depletion extending right to the bottom.

In 1930–31, between the cruises of December 4th and January 13th, phosphate fell by 10 mg. (surface) and 3·1 mg. (average). The surface fall was, in large part, due to the mixing in of the enriched surface layer found on December 4th, but the fall in the average content would seem to indicate a definite outbreak. Over the whole intervening period of 39 days, sunshine averaged 2·1 hours per day and B^3 averaged 51. For the nine days immediately preceding January 13th, sunshine averaged 4·3 hours and B^3, 14. But for this period the parallel between quiet sunny weather and a plankton outburst may not be as close as this summarised picture suggests.

On November 30th, 1931, at four stations across the Channel, L4, E1, Midway, and E2, surface values for phosphate as P_2O_5 were 5·5–7 mg. lower than at 5 metres, suggesting a preceding, quiet, sunny spell. This was far from being the case. Between November 22nd and 29th daily mean cube Beaufort numbers were : 63, 301, 53, 259, 215, 105, 3, 23. Such a period of wind must have led to thorough mixing of the surface waters. Two days only were sunny and the last two days, which were quiet, had only 0·7 hours of sunshine between them. The weather was thus decidedly unfavourable for a plankton outburst.

We see that on three occasions, midwinter outbursts, inferred from a fall in the phosphate content of the water, followed on periods of sunny weather with light winds. On a fourth occasion there was no relation whatever between outburst and weather.

The Effect of Wind on the Bottom Fauna and on the Herring Fishery.

On January 5th, 1933, s.s. *Salpa* caught large numbers of *Upogebia deltaura* and *Thyone raphanus* with the otter trawl in 18–21 fathoms in Bigbury Bay. Examination of the gut of fishes has shown Upogebia to be one of the commonest fish foods in the Plymouth area, but it is seldom caught in numbers in either trawl or dredge (Steven, 1930). It is an agile burrowing animal beyond the reach of the ordinary fishing-gear. The habitat of Thyone is similar. Therefore only intense disturbance of the bottom could have put them in a position to be caught by the trawl. Probably Upogebia had been so buffeted by the storm as to be insensible to the approaching trawl. December was characterised by very stormy weather and between December 31st and January 4th, the daily mean cube Beaufort number reached 350 and never fell below 216. In other words the wind blew continuously with force 6 or greater, causing heavy seas and consequent disturbance of the bottom fauna (Fig. 1, C.).

Periods of stormy weather have been found to be followed by improved catches of herring (Ford, 1933). For this investigation, wind records on the Beaufort scale proved very useful, but it is felt that the mean cube Beaufort number, studied in conjunction with the direction of the wind, may prove yet more convenient as it emphasizes the periods of really rough weather. When dealing with large quantities of weather data, the possibility which it gives of grouping or averaging records may prove of value.

SUMMARY.

In August, 1932, marked stratification of the water in the English Channel led to an unusual distribution of minor chemical constituents. Two thermoclines were present, between which high silicate values were found, indicating rapid re-solution of silica as found in former summers; pH was also very high at 15 metres.

In or about December in four years, nitrite in inshore waters has been found much in excess of that present in the open Channel.

The "mean cube Beaufort number" is suggested as a useful practical measure of sea disturbance. Three out of four midwinter plankton outbursts, inferred from a fall in the phosphate content of the water, have followed periods of sunny weather with little wind.

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The Rapid Estimation of the Copper Content of Sea-water.

By

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The recent recognition of the importance of copper in nutritional anæmia and the work of Prytherch (1931) on its unique action in stimulating oyster larvæ to become attached have rendered the analytical determination of minute amounts of copper a matter of some interest.

In a former paper (1932) it was shown that the copper present in sea-water could be concentrated by electro-deposition and subsequently redissolved and estimated colorimetrically using sodium diethyl-dithiocarbamate according to the method of Callan and Henderson (1929).

In this the deposition required three hours at 90°–100° C., though but little attention was necessary during that period.

Another method of concentration has since been tried, in which, after adding the 0·1 per cent aqueous solution of the reagent and allowing a few minutes for the colour to develop, the coloured compound is extracted with an organic solvent. For this purpose the chemists of the British Drug Houses Ltd., who introduced the method, recommend chloroform, carbon tetrachloride, or other immiscible solvent.

This method is useful in testing coloured solutions containing copper and obviously increases the delicacy; it has been found to do so to an extent which renders the method suitable for direct use with sea or river water, though unlike sea-water, river water can be concentrated greatly by evaporation if necessary. Furthermore, it has been found that only a trace of the yellowish or brownish colouring matter present in the fresh or brackish waters examined is imparted to chloroform when shaken up with the sample. Iron salts give with the reagent a colour rather like that produced by copper. The presence of much iron would accordingly render the results erroneous, though it requires 1·32 mg. per litre of ferric iron to give as much colour as 0·01 mg. per litre of copper. Only in fresh water would there be any risk of error from iron.

The analysis is made by adding 10 ml. of reagent to 100 or 200 ml. of sample and after about ten minutes the process of extraction is carried out by adding 10·0 ml. of chloroform to 100 or preferably 200 ml. of the sample in a separating funnel. The mixture is shaken violently by hand for exactly two minutes and allowed to stand. The chloroform extract is then drawn off into one of the colorimeter cups and suffices to fill it to a depth of about 52 mm. The other cup receives a similar extract, but made from a standard solution containing 0·01 mg. of copper in 100 ml., or twice that amount in 200 ml. The same volume of sample and standard should always be extracted.

It is advisable also to make a blank extraction of the sample, without reagent, as traces of the brown or yellowish substances which colour fresh waters are taken up, also the pigment may be partly extracted from plankton present. It has been found that a colorimeter setting of 2·0 mm. of the standard can just be distinguished from 50·0 mm. of pure chloroform. The blank given with pure sea-water is the same, 2 mm., whereas the water of the River Yealm, a moorland river of brownish colour, gave as blank 5·2 mm. and the clear yellowish water of the Conway River, at low tide (sp. gr. 1·001), gave only 5·5 mm. On the other hand apparently colourless water from an oyster tank gave 6·5 mm. blank, equivalent to 0·0013 mg. copper in 100 ml., or 13 mg. per cubic metre.

Larger volumes, up to 1 litre, may be extracted if necessary. Even with only 200 ml. and 10 ml. of solvent, the removal of the coloured copper compound is by no means complete; further extraction will remove colour not only from the liquid, but from the droplets of the organic solvent which adhere to the walls, so it is not easy to ascertain the percentage left behind after one extraction. This does not however vitiate the results provided the extractions are carried out in an identical manner for sample and standard.

Determinations carried out as described, using 100 ml. or 200 ml. samples, gave the following results, expressed in milligrams of copper per cubic metre :

Conway River, high water 16, low water 36. River Exe, at Lympstone, Exmouth, high water 8, low water 14. River Yealm, not tidal, 0. A non-moorland tributary stream of River Yealm, 5. The oyster tanks at Lympstone and Conway varied from 0–15. None of the figures here given are of significance in bringing about the attachment of oyster larvæ, which, according to Prytherch, settle down when the copper content of the water lies between 150 and 500 mg. per cubic metre. This range contained 97·5 per cent of the larvæ he observed, with *Ostrea virginica.* The British species is *O. edulis* and may behave differently. I am indebted to Mr. H. P. Sherwood of the Conway Fisheries Experiment Station for kindly providing me with a number of water samples.

As regards the solvent used for extraction, McFarlane (1932) states that chloroform and carbon tetrachloride are unsatisfactory, but he gives no reason. He recommends the purest amyl alcohol as the colour of the extract fades with the “ technical ” variety. In chloroform solution fading has never been suspected to occur within the usual duration of a day's work, nor has the solvent proved unsatisfactory, save as regards the incompleteness of a single extraction. Evaporation of the solvent must be guarded against.

In order to compare the solvents chloroform, carbon tetrachloride, and amyl alcohol, 10·0 ml. of each was added to 100 ml. of Plymouth tap water, using ordinary methylated chloroform, carbon tetrachloride "purified," and amyl alcohol "analytical reagent, pyridine and nitrogen free." The soft tap water has a brownish tint of which amyl alcohol extracted between four and five times as much as did either of the others, this of course is a disadvantage. Of the 10 ml., the amounts recovered were, respectively, 8·7, 9·8, and 6·9 ml. after standing overnight.

With 200 ml. of sea-water and 10·0 ml. of solvent the volumes recovered were respectively 7·4, 9·7, and 4·0 ml. The alcohol floats, which is a disadvantage, as the large volume of sea-water has to be drawn off from the separating funnel before it, whereas the other two sink and time is saved in drawing them off. The concentration of copper compound in the alcohol is about 1·5 times, and in the tetrachloride 0·66 times that in chloroform ; but taking into account the volumes recovered, that in the tetrachloride is almost exactly the same as in chloroform, whereas only 0·8 times as much is obtained with the alcohol. The comparisons were made after standing overnight. The alcohol does not separate as readily as do the others, but separates from sea-water better than from fresh.

SUMMARY.

1. The copper content of sea and river waters can be rapidly determined using the sodium diethyl-dithiocarbamate method followed by extraction with chloroform.

2. This solvent takes up only traces of the natural colouring matters found in waters, but blank estimations should be made with some river waters and occasionally with sea-waters on account of the presence of plankton.

3. Carbon tetrachloride can be used instead of chloroform as solvent, it extracts less per unit volume, but the volume recovered is larger, the resultant yield being identical. Amyl alcohol extracts more than chloroform, but the volume recovered is smaller, the resultant yield being about 0·8 times that of the others. The alcohol takes up more colouring matter from river water, does not separate as readily as the others, and floats, whereas they, more conveniently, sink. For work in hot climates its higher boiling-point may be an advantage.

4. In fresh water iron salts in large excess might cause error ; this can be checked by the electro-deposition method.

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The Use of Cuprous Oxide and other Rectifier Photo Cells in Submarine Photometry.

By

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With 1 Figure in the Text.

THE cuprous oxide cell introduced by Lange (1930) differs greatly from the photo-electric cells heretofore in general use. The sensitivity is high and no high-tension battery is needed in the circuit. There are, however, certain limitations to the use of such rectifier cells for daylight photometry; these we have considered elsewhere (1933). The types dealt with include cuprous oxide cells of both French and German origin and a selenium rectifier cell, introduced by Bergmann (1931) and made by the Süddeutschen Apparate-Fabrik, Nürnberg, and under license by the Weston Electrical Company, from which our cell was obtained. The latter arrived too late for use in submarine measurements in the summer of 1932, but is to be preferred to the cuprous oxide type. There is another type of rectifier, the Bernheim cell, which is made in Paris. This we have not examined as yet, but from data supplied by the makers its spectral sensitivity is similar to that of the Bergmann cell, which it also resembles in its high sensitivity and improved stability.

THE SUBMARINE PHOTOMETER.

This was intended for shore work, so that it could be carried about in a diver's hand. It consists of a circular gun-metal box, 9·6 cm. diameter, flanged at the top and fitted with a ring; between ring and flange a 0·6 cm. disc of plate glass was fitted and secured. Above this the usual disc of opal flashed glass could be placed, with a colour filter in between if so desired. Two of the flange screws had projections with holes for attaching a light rope.

A "Serpidox" photo-electric cell, Sx80, obtained from the Société de Recherches et de Perfectionnements Industriels, Puteaux (Seine), was mounted immediately below the window, and beside it a small amount of calcium chloride was held in a bag.

The cable entered through a side tube with slightly bulbous nozzle, a water-tight joint being effected by means of thick pressure tubing. Six hundred megohm "cab-tyre" twin cable was used; a length of 45 m. sufficed for the coastal work and weighed 4·5 kg. The photometer weighed 3·2 kg., as against 22 kg. the weight of that formerly in use at sea. It was reported as convenient to hold and not too heavy under water.

The Air Photometer, Galvanometer, Shunt, and Connections.

A similar "Serpidox" cell, No. Sx81, was used to measure the illumination in air. It was placed on a level rock, unmounted, but covered with the usual opalized glass and a water filter to lessen temperature errors. Both photometers were connected to a throw-over switch and to the special shunt. When received the two Serpidox cells were closely the same in sensitivity, but when mounted in the submarine photometer the greater distance of the cell from the opal resulted in the ratio of the readings in air, when both were under water screens, being on the average 0·75.

For measuring the current we found a Cambridge Instrument Co. "Versatile Galvanometer," weighing 1·8 kg., to be suitable. Its resistance is 10 ohms, and each scale division corresponds to $2\mu a$; the scale (upper) reads to 120, viz. $240\mu a$. With this instrument we made use of a shunt, specially designed to keep the resistance 10 ohms always; this permitted the ranges 1, 5, 10, and 50 to be used, and is figured in our previously mentioned paper.

The Standardization of the Photometers.

In view of the lack of strict proportionality between current and intensity and of the change of sensitivity with time and exposure, it is necessary to standardize each cell against a vacuum photo-electric cell of the usual type. This was done on the Laboratory roof, over an extended range, using the potentiometer method. Low intensities were measured in a north window, using a galvanometer instead of a potentiometer. The Serpidox cell was connected to the 10-ohm galvanometer throughout. The results are shown in Figure 1, curves A and B.

As the change of sensitivity with time may depend on the intensity, the sensitivity of the cell should be checked at two or three different sensitivities from time to time.

From the form of the voltage curve, C, obtained with the rectifier cell connected directly to the No. 2 circuit of the potentiometer outfit, but with the vacuum cell connected as usual, it may be seen that this cell could be used at sea with the potentiometer outfit, viz. under conditions precluding the use of ordinary galvanometers. Illuminations can be read off from the curve, though indeed for low illuminations up to 10,000 metre candles, the deviation from a straight line is but slight in the case of a Serpidox cell. Those of other types give marked curvature in bright light on open circuit.

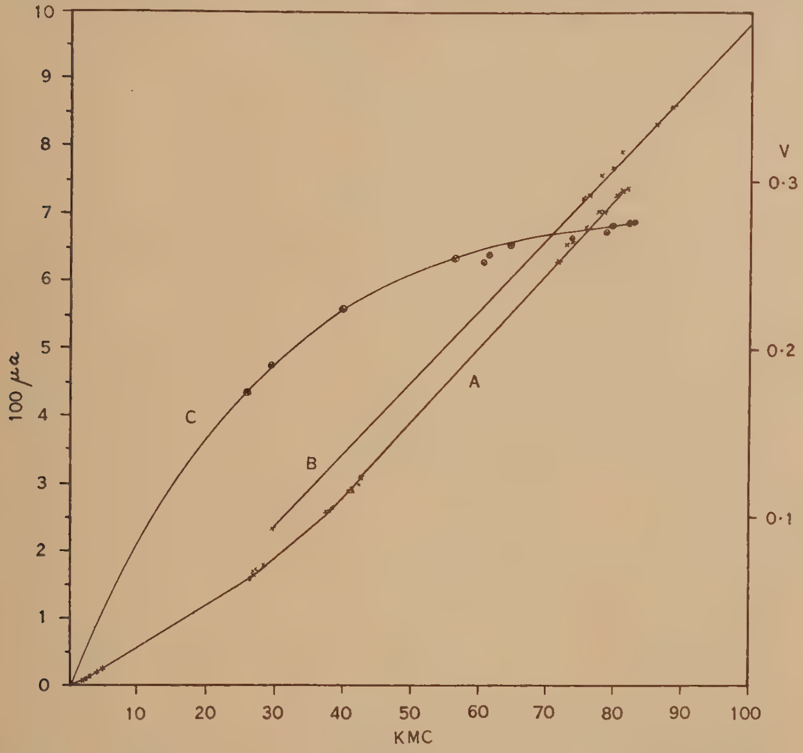

Fig. 1.—The abscissæ show vertical illuminations in thousands of metre candles (k.m.c.). The left-hand ordinates show current in $100\mu a$ units. The right-hand ordinates show E.M.F. in volts on open circuit.

Curve A gives the behaviour of a cuprous oxide cell (Sx81) when cold, curve B when the sun had warmed it up, though under a water heat filter. Curve C shows the voltage relation, as determined with the submarine potentiometer outfit, measuring illumination with vacuum cell and taking the voltage of the cuprous oxide cell directly connected to the No. 2 circuit.

The sensitivity with the voltage measurement is about the same as with the low resistance galvanometer, for approximately 10,000 m.c. gives $200\mu a$ or 0·0800 volts. The former can be read to $0{\cdot}2\mu a$ or 10 m.c., the latter to 0·05 m.v. or 6·2 m.c. Voltage readings with "open circuit" or high resistance instruments are, however, more affected by temperature errors than current measurements with a low resistance galvanometer.

In carrying out such open-air standardizations one is faced with the problem of the variation of the light, which is rarely constant from one minute to another. The steadiest light is obtained with a clear sun and a clear blue sky at noon, or with a clear sun and clouds moving slowly. A hazy sky is liable to considerable variation in the degree to which the sun is obscured and a grey sky is normally very variable. Good results can be obtained, as at sea, by taking the average of a series of potentiometer readings for each photometer, or on land by two observers reading galvanometers simultaneously. In the standardizations shown in curve C, series of potentiometer readings were made, but for curves A and B one observer made absolutely simultaneous observations by sound and sight ; as the galvanometer was read the potentiometer dial was adjusted to minimum sound in the telephone, then after dictating the reading the potentiometer scale was read. Owing to the difference in the colour sensitivity of the potassium and the copper oxide rectifier cells the ratio of the sensitivities will depend on the relative amount of sunlight, much as when the CMV6 type of cell is being standardized.

We cannot, however, use the readings of the submarine photometer, after standardization against the air photometer (both under water screens), to measure the illumination at various depths in the sea without introducing a factor to correct for reflection losses at the surface of the opal and internal reflection effects in the opal and between it and the surface of the sea. These we have considered fully elsewhere (1933, a). The illuminations recorded have to be multiplied by a factor 1·09 in order to give the true under-water values. Thus, since the submarine photometer was less sensitive than the air photometer, even in air, its readings must be multiplied by 1·33 to make the two agree. When the submarine photometer is in water a further factor 1·09 must be used to correct for surface effects. The procedure is to read off the illumination, on the figure, for the current given by the submarine photometer and *then* to divide this reading by 0·75 and to multiply it by 1·09, or in one operation to multiply by 1·45. For example, a reading of $200\mu a$ corresponds for the air photometer to 31·0 thousand metre candles (k.m.c.), but for the submarine photometer, when submerged below about 10 cm. or any greater depth, $200\mu a$ corresponds to $31{\cdot}0 \times 1{\cdot}45 = 44{\cdot}9$ k.m.c. Were we, however, to multiply the current ($200 \times 1{\cdot}45 = 290\mu a$), and then to read off from the figure, the result would, incorrectly, be 41·0 k.m.c. The difference is due to the curvature in the current illumination relation. In a similar manner submarine illuminations may be obtained from the voltage-illumination curve, but in this case the departure from a rectilinear relationship is very marked. For use under damp conditions, such as would arise where a cabin was not available on a ship or in northern latitudes, the fact that high insulation is no longer necessary and "dark currents" are negligible, since no high-tension battery is required, must be regarded as greatly favouring the use of this type of cell. Under normal conditions on a ship the ordinary vacuum cells have so much to recommend them in the way of greater accuracy that it would seem wise, for the present at any rate, to continue to use them. For approximate work on the coast, where the illumination is of necessity very variable, the cuprous oxide or other rectifier type of cell has the great advantage of portability in the measuring apparatus required, and the cell itself is quite accurate enough, if its limitations are remembered ; it requires, of course, to be standardized against a vacuum cell.

We are indebted to Mr. J. A. Kitching and to Mr. G. Gilson for descending with a diving helmet on the coast near Wembury, Devon, and holding the photometer in positions of ecological interest. The results will be presented by them in their survey which includes the percentage of the diffuse light in air, as determined at a given tidal level, found where various algæ, Himanthalia, Laminaria, etc., were growing. From measurements of the coefficient of absorption of the water, the illumination in the different zones could be calculated for other states of the tide. The absorption coefficient would increase greatly in rough weather and decrease in very calm weather, but during the diving operations on August 3rd, 1932, it was about 0·5, for vertical absorption. The figure is unduly high owing to diminution of light, not only by absorption, but by shading from the sides of the rocky gully investigated. We have, however, found water close to shore in rough weather to have $\mu_v = 0{\cdot}8$ and even in very calm weather one could hardly expect it to be lower than 0·3, a value occasionally reached several miles out at sea. The date mentioned was the first that was possible for diving on such an exposed coast, after a period of stormy weather.

SUMMARY.

1. Photo-electric cells of the rectifier type are useful for approximate measurements of light intensity, in air or under water, using a low-resistance galvanometer, the current through which may be reduced by a special shunt keeping the circuit resistance constant.

2. Such an arrangement has proved serviceable for shore work, a light gun-metal photometer, housing a cuprous oxide cell, having been carried about by a diver.

3. These rectifier cells can also be used at sea, but instead of the current, the E.M.F. is determined by means of the potentiometer outfit as used at sea in previous years.

4. The current-illumination relation is not rectilinear over a wide range of intensity; the current–voltage relationship shows very marked curvature.

5. The cuprous oxide cells have a considerable temperature coefficient and must be used with a water screen. The coefficient is smaller in the case of the selenium cell. Under prolonged exposure to light the sensitivity of the cuprous oxide cell decreases very considerably, but the selenium rectifier cell is far more stable.

6. Further laboratory and sunlight tests carried out with the Bergmann selenium cell while this paper was in the press, give great promise as to its suitability and convenience for daylight measurements in the field and under water, when due allowance is made for the curvature of its illumination: current characteristic.

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The Seasonal Distribution of Macroplankton as shown by Catches in the 2-metre Stramin Ring-trawl in Off-shore Waters off Plymouth.

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In past years during the study of the vertical distribution of macroplankton much information has been obtained on the abundance of the different animals in the catches at different times of the year. Results have already been published to show the seasonal distribution of pelagic young fish (**4**), and also on the abundance and composition of the Sagitta population (**5**, p. 565). In this latter study the change over from the predominance of *Sagitta elegans* to that of *S. setosa* during the years 1930 to 1932 is striking. During the examination of catches it has been noticed that each year has been characterised at some time by the abundance of a species which may occur only in small numbers, if at all, in other years. This has been especially noticeable in the composition of the medusa population. It is necessary to follow these changes through a number of years to see if the presence of certain plankton organisms cannot be used as an index of conditions that may lead to other fluctuations such as those of the fisheries.

During 1930 and part of 1931 weekly catches of the 2-metre stramin ring-trawl were counted in order to obtain precise information on the seasonal abundance of the different animals throughout a whole year. The collections were made by oblique hauls of half an hour duration at the station 2 miles east of the Eddystone (**4**). Counts were made as on previous occasions by picking out directly distinctive and unusual animals and counting every animal in a $\frac{1}{10}$th sample of the remainder (**2**, p. 776).

The full results are given in the attached table which gives instructive information on the seasonal variation in abundance of the different animals, and their relative importance in numbers one to another. It seems unnecessary to analyse the tables further since any worker can abstract from it the data he may desire. One or two points must, however, be borne in mind.

1. The animals are all of a size that is normally retained in good condition by the stramin net. For instance, the medusæ are generally well-grown individuals; the earliest stages, while perhaps not small enough to pass through the meshes, are generally too badly damaged to allow of

definite identification. A useful indication of the size of disregarded medusæ is given by the absence of *Rathkea octopunctata* in Table I, which is common in tow-nettings in the earlier months of the year. This applies also to all other animal groups; the earliest stages of decapod larvæ do not appear in numbers in the catches as many will pass through the meshes.

In considering the seasonal distribution of any animal it must therefore be remembered that its first appearance in the catches does not imply the actual beginning of its abundance in the plankton. A period of two or three weeks should be allowed for the growth of the earliest stages to a size sufficient to appear in the catches.

2. The table does not contain any data on the abundance of young fishes which has been dealt with in another report (**4**).

3. In examining the data the vertical distribution of the various animals must be considered. The figures for *Tomopteris helgolandica* show, for instance, a great increase in July and August. This must only be regarded as an increase in abundance in the plankton; at other times the Tomopteris may actually be present in the area, but in the unsampled layers very near the bottom (see **3**, from which data can be obtained for most of the animals).

4. The names given in the table are those used in the Plymouth Marine Fauna (1931). Phialidium sp. will be mostly *Phialidium hemisphæricum : Phialella cymbaloides* will also occur though not so commonly, as also a few *Mitrocomella brownei*. It was not possible in the time to analyse all the Decapod larvæ into species: the species that comprise each group can be found in the Plymouth Marine Fauna, where also in many cases is given the time of year at which the larval stages are most prevalent. Pandalid larvæ must be taken to include all species contained under Pandalidæ, Hippolytidæ, and Processidæ. Mysid sp. in summer consist chiefly of young specimens.

5. Examination of catches over a number of years has shown that there are species which can normally be expected to appear regularly each year. It is felt that these results are a fairly reliable picture of the average ring-trawl plankton catches to be found throughout any year. The following species, however, appeared in exceptional numbers and cannot be regarded as characteristic, but only for the year in question at the times they appeared :—

Aglantha rosea, *Liriope exigua*, and *Stephanomia bijuga* : *Clione limacina* and adult *Meganyctiphanes norvegica* also appeared in unusual numbers at the beginning of the year, although the larvæ of the latter are usually present then.

The results are to form a basis with which future years can be compared. Marked differences have been noticed in other years and it is hoped to publish these results in a separate report when sufficient data have been gathered. It should then be possible to decide on certain species whose appearance in the plankton should be watched for in future years. It is especially desirable to see whether any correlation can be found between the appearance of one characteristic species and that of another. The desirability of such observations was already stressed many years ago when Allen (**1**) prepared a list of species for special observation. Now that regular collections of these larger plankton animals are obtainable throughout the year an opportunity is afforded to attempt this study over a period of a number of years.

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TABLE I.

NUMBERS OF ANIMALS IN HALF-HOUR OBLIQUE HAULS WITH THE 2-METRE STRAMIN RING-TRAWL TAKEN 2 MILES EAST OF THE EDDYSTONE.

1930.	Dipurena (Slabberia) halterata.	Steenstrupia nutans.	Bougainvillia sp.	Amphinema dinema.°	Leuckartiara octona.	Laodicea undulata.	Cosmetira pilosella.	Obelia sp.	Phialidium sp.	Saphenia gracilis.	Aequorea forskalia	Aglantha rosea.	Liriope exigua.	Muggiaea atlantica.	Stephanomia bijuga.	Chrysaora isosceles.	Cyanea lamarcki.	Aurelia aurita.	Pleurobrachia pileus.	Beroe cucumis.	Peachia arvæ.	Arachnactis larvæ.
Feb. 4th . .	–	–	–	–	–	–	–	–	–	–	–	52	–	–	–	–	–	–	40	–	–	–
,, 12th . .	–	–	–	–	–	–	–	–	–	–	–	2	–	–	880*	–	–	–	80	–	–	–
,, 19th . .	–	–	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	3	–	–	–
,, 26th . .	–	–	–	–	–	–	–	–	–	–	–	8	–	–	1	–	–	–	3	–	–	–
Mar. 5th . .	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	6	2	–	–
,, 12th . .	–	–	–	–	–	–	–	–	–	–	–	2	–	–	800*	–	–	1†	10	2	–	–
,, 19th . .	–	–	–	–	–	–	–	–	–	–	–	–	–	–	210*	–	–	–	8	–	–	–
,, 27th . .	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–
April 2nd . .	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
,, 11th . .	–	–	–	–	–	–	–	–	40	–	–	7	–	–	632*	–	1	–	7	–	–	–
,, 16th . .	–		–	–	–	–	–	–	20	–	–	20	–	–	190*	–	–	–	1	–	–	–
,, 24th . .	–	–	–	–	1	–	–	–	140	–	–	7	–	–	450*	–	6	–	–	–	–	10
,, 29th . .	10	–	–	–	3	10	330	–	140	40	–	10	–	–	370*	1	1	–	10	–	–	–
May 7th . .	1	–	–	–	8	24	10	–	386	–	–	–	–	–	–	–	2	–	193	–	3	4
,, 15th . .	–	–	320	–	40	–	140	1,680	760	100	–	40	–		2,460*	–	1	–	520	–	–	41
,, 22nd . .	–	–	150	–	93	5	5	40	100	10		90	2		760*	–	1	–	520	–	1	–
June 10th . .	–	–	60	10	430	–	–	80	50	11	–	850	–	–	–	–	–	–	100	–	–	5
,, 19th . .	–	1	–	10	179	10	–	260	140	1	–	1,000	1	–	–	–	3	–	68	–	20	1
,, 26th . .	–	60	261	–	280	20	250	1,025	1,340	1	–	5,736	–	–	1,640*	–	1	–	180	–	2	2

July 4th	–	–	161	–	129	–	180	800	920	–	–	1,932	–	–	–	–	–	–	80	20	4	–
,, 9th	–	120	–	–	270	–	600	43,800	3,780	90	–	6,150	1	–	30	–	–	–	–	120	15	–
,, 14th	–	–	–	1,110	180	–	180	24,540	2,970	90	–	11,040	–	–	–	–	–	–	–	30	94	–
,, 23rd	–	–	–	330	180	–	1,530	1,080	5,790	150	1	28,440	–	–	–	–	2	–	–	21	127	–
,, 29th	–	–	–	990	60	–	870	810	3,750	–	–	23,040	–	–	–	–	3	–	–	39	35	–
Aug. 7th	–	–	–	–	150	300	–	330	1,620	–	1	40,020	–	–	–	–	–	–	–	26	–	–
,, 14th	–	–	–	1	44	120	60	160	4,020	40	–	33,220	446	–	–	–	–	1	–	137	–	–
,, 21st	–	6	–	–	9	500	–	–	3,240	28	–	8,360	17,442	20	641*	–	–	–	–	33	–	–
,, 28th	–	–	–	–	120	3,240	–	–	2,540	20	–	3,540	7,440	20	2*	–	–	–	–	32	–	–
Sept. 3rd	–	1	–	–	92	9,800	–	80	180	80	–	1,080	11,600	20	40*	–	–	–	1	8	17	–
,, 11th	20°	–	–	–	21	4,160	–	100	4,300	–	–	340	4,280	–	–	1	–	–	161	33	55	–
,, 16th	–	–	–	–	53	2,310	10	30	100	–	–	51	2,800	30	–	–	–	–	220	6	20	–
,, 24th	–	–	–	–	77	10	–	–	640	–	–	180	3,760	20	–	–	–	–	800	4	–	–
Oct. 1st	–	–	–	–	18	–	–	–	60	–	–	50	180	–	–	–	–	–	1,370	3	–	–
,, 7th	–	–	–	–	3	–	–	–	340	–	–	20	660	–	–	–	1	–	500	4	–	–
,, 14th	–	–	–	–	–	–	–	20	510	–	–	–	4,100	20	–	–	–	–	–	–	–	–
,, 16th	–	–	–	–	–	–	–	10	330	–	–	–	1,680	–	–	–	–	–	–	–	–	–
Nov. 6th	–	–	–	–	–	–	–	–	20	–	–	–	1,650	–	–	–	–	–	–	–	–	–
,, 13th	–	–	–	–	10	–	–	–	20	–	–	–	980	50	–	–	–	–	20	–	–	–
,, 20th	–	–	–	–	–	–	–	–	10	–	–	10	1,390	10	–	–	–	–	–	–	–	–
,, 26th	–	–	–	–	–	–	–	–	10	–	–	–	710	10	–	–	–	–	–	–	–	–
Dec. 3rd	–	–	–	–	–	–	–	–	100	–	–	–	1,115	–	–	–	–	–	10	–	–	–
,, 10th	–	–	–	–	–	–	–	–	20	–	–	–	1,020	20	–	–	–	–	1	–	–	–
,, 17th	–	–	–	–	–	–	–	–	–	–	–	–	690	50	–	–	–	–	–	–	–	–
,, 22nd	–	–	–	–	–	–	–	–	–	–	–	–	140	10	–	–	–	–	–	–	–	–
1931.																						
Jan. 1st	–	–	–	–	–	–	–	–	–	–	–	–	310	130	–	–	–	–	–	–	–	–
,, 5th	–	–	–	–	–	–	–	–	–	–	–	–	230	170	–	–	–	–	–	–	–	–
,, 15th	–	–	–	–	–	–	–	–	70	–	–	–	970	1,166	–	–	–	–	–	–	–	–
,, 22nd	–	–	–	–	–	–	–	–	30	–	–	–	104	130	–	–	–	–	–	–	–	–
,, 26th	–	–	–	–	–	–	–	–	–	–	–	–	10	10	–	–	–	–	–	–	–	–
Feb. 6th	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–
,, 12th	–	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–	1†	–	–	–	–
,, 20th	–	–	–	–	1	–	–	–	10	–	–	–	–	30	–	–	–	–	–	–	–	–
,, 23rd	–	–	–	–	20	–	–	–	80	–	–	–	2	–	–	–	–	–	–	–	–	–
‡Mar. 17th	–	–	–	–	2	–	–	–	1,820	–	–	–	–	–	–	–	20	–	–	–	–	–
,, 26th	–	–	–	–	10	30	–	70	4,520	–	–	–	–	180	–	–	16	–	–	–	–	–
April 1st	–	–	–	–	2	–	20	–	220	–	–	–	–	20	–	–	3	–	20	–	–	–
,, 16th	–	–	–	–	–	–	660	–	12,120	–	–	–	–	–	–	–	23	–	40	–	–	1,480

° Possibly a few *A. rugosa*. ‡ Medusæ only counted. * Nectophores. † Ephyra.

TABLE I—*continued.*

1930.	Tomopteris helgolandica.	Terebellid larvæ.	Pœcilochætus serpens larvæ.	Sagitta elegans.	Sagitta setosa.	Calanus finmarchicus.	Euchæta hebes.	Metridia lucens.	Candacia armata.	Anomalocera patersoni.	Labidocera wollastoni.	Caligus sp.	Mysid sp.	Nyctiphanes couchii adult.	Euphausiid larvæ.	Meganyctiphanes norvegica.	Apherusa sp.	Hyperia galba.	Themisto gracilipes.	Idotea sp.	Cumacea.
Feb. 4th .	140	2	–	11,360	–	1,200	–	–	20	–	–	–	100	4,218	–	150	–	–	112	–	–
,, 12th .	770	–	–	16,270	130	540	–	–	–	–	–	1	–	–	380	–	–	–	–	–	–
,, 19th .	251	–	–	10,411	389	1,280	–	–	60	–	–	1	–	20	–	–	–	–	1	–	–
,, 26th .	3	–	–	452	110	580	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mar. 5th .	165	–	–	1,517	93	450	–	–	–	–	–	–	–	4	–	–	–	–	1	–	–
,, 12th .	33	–	–	455	5	260	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
,, 19th .	–	–	–	8	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
,, 27th .	3	–	–	1,860	–	420	–	–	–	–	–	2	–	2	–	–	–	–	–	–	–
April 2nd .	–	–	–	24	1	10	–	–	–	38	–	1	–	–	–	–	–	–	1	–	–
,, 11th .	3	–	–	240	–	440	–	60	–	–	–	1	–	2	–	–	–	–	–	–	–
,, 16th .	–	–	–	21	–	16,890	–	70	60	30	–	1	–	1	310	1	–	–	–	–	–
,, 24th .	–	–	10	860	–	7,630	–	–	510	–	–	1	–	–	1,140	–	–	–	130	–	–
,, 29th .	–	–	–	39	1	960	–	60	80	–	–	–	–	1	540	–	–	–	2	–	–
May 7th .	7	386	–	77	2	318,450	–	193	772	–	–	–	–	2	2,702	–	–	–	–	3	–
,, 15th .	10	60	–	243	7	24,720	–	80	260	–	–	–	–	–	580	–	–	–	–	–	–
,, 22nd .	10	–	–	101	–	11,210	–	–	50	20	–	1	–	–	450	–	–	–	–	–	–
June 10th .	63	–	110	1,324	–	1,968	–	–	200	4	–	1	1	4	40	–	–	–	–	–	–
,, 19th .	25	–	–	637	6	6,592	–	–	220	22	–	2	–	–	20	–	–	5	–	–	–
,, 26th .	95	–	–	760	–	3,560	–	40	320	13	–	2	2	–	40	–	20	–	20	–	–
July 4th .	10	–	–	2,218	–	2,023	–	–	200	62	–	2	2	–	–	–	20	–	1	–	–
,, 9th .	664	–	–	4,377	8	6,132	–	–	2,160	60	–	2	360	–	–	–	60	–	1	–	–
,, 14th .	741	–	–	3,942	4	8,370	–	–	930	†	–	–	152	–	30	–	–	–	–	–	–
,, 23rd .	759	–	30	2,142	10	2,910	–	30	1,860	10	–	2	60	8	30	–	750	–	–	–	–
,, 29th .	376	–	–	1,423	12	1,007	–	30	270	–	–	4	6	–	–	–	240	–	1	–	–

Aug. 7th .	1,602	–	–	7,800	36	2,730	–	–	450	–	–	5	94	102	–	–	30	–	1	–	–
,, 14th .	222	1*	–	5,210	5	1,041	–	–	220	1	–	8	17	–	140	–	200	–	1	–	–
,, 21st .	42	1†	–	2,038	–	803	–	–	200	–	–	4	–	–	20	–	240	–	21	–	20‡
,, 28th .	4	–	–	1,018	–	402	–	–	80	–	–	1	–	–	–	–	140	–	22	–	–
Sept. 3rd .	179	–	–	1,222	47‖	363	–	–	140	1	–	–	20	–	–	–	360	–	1	–	–
,, 11th .	–	–	–	4,398	760	612	–	–	560	3	–	7	–	1	20	–	100	–	25	–	–
,, 16th .	26	1°	–	558	46	233	–	–	40	1	10	–	–	–	–	–	–	–	3	–	–
,, 24th .	4	–	–	270	87	35	–	–	–	53	–	–	–	–	7	–	–	–	2	1	–
Oct. 1st .	8	–	–	102	45	70	–	–	20	–	–	1	–		–	–	–	–	2	–	–
,, 7th .	–	–	–	74	369	263	–	–	30	–	–	1	–	–	–	–	–	1	–	–	–
,, 14th .	3	–	–	303	683	–	–	–	150	–	–	2	1	–	–	–	–	–	–	–	–
,, 16th .	1	–	–	229	258	118	–	–	10	10	–	–	–	–	–	–	–	–	–	–	–
Nov. 6th .	–	–	–	441	300	–	–	–	10	–	–	1	1	–	–	–	–	–	–	–	5
,, 13th .	–	–	10	159	120	99	–	–	40	–	–	–	–	1	10	–	–	–	–	–	–
,, 20th .	–	1**	–	32	73	7	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
,, 26th .	1	–	–	61	84	14	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–
Dec. 3rd .	–	–	–	730	1,080	107	–	–	40	–	–	1	–	–	–	–	–	–	–	–	–
,, 10th .	–	–	–	360	162	129	–	–	100	–	–	1	–	–	121	–	–	–	1	–	–
,, 17th .	–	–	–	262	372	169	–	–	70	–	–	–	–	–	30	–	–	–	1	–	–
,, 22nd .	–	–	–	72	78	98	–	–	90	–	–	–	–	–	10	–	–	–	–	–	–
1931.																					
Jan. 1st .	1	–	–	210	249	20	–	–	60	–	–	2	–	–	–	–	–	–	–	–	–
,, 5th .	–	–	–	109	59	80	10	–	120	–	–	1	–	–	10	–	–	–	–	–	–
,, 15th .	1	–	–	1,765	339	190	–	–	150	–	–	–	10	3	–	–	–	–	–	–	–
,, 22nd .	–	–	–	172	270	56	–	–	20	–	–	1	–	–	8	–	–	–	–	–	–
,, 26th .	–	–	–	117	101	19	10	–	20	–	–	–	–	–	7	–	–	–	–	–	–
Feb. 6th .	–	–	–	51	2	–	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–
,, 12th .	–	–	–	83	17	40	–	–	10	–	–	1	–	–	–	–	–	–	–	–	–
,, 20th .	–	–	–	816	239	446	–	–	220	–	–	1	–	–	–	–	–	–	–	–	–
,, 23rd .	–	–	–	474	134	343	–	–	420	–	–	1	–	–	20	–	–	–	–	–	–
Mar. 17th .	7			7,502	221									36			Rest of sample not counted				
,, 26th .	25	321††	–	491	333	110	–	–	50	–	–	3	–	–	–	–	–	–	–	–	–
April 1st .	–	60	–	935	1,048	320	–	–	220		–	–	–	–	–	–	–	–	–	–	–
,, 16th .	30	200	–	764	385	1,260	–	–	180	–	–	1	–	–	–	–	40	–	–	–	–

* Young Syllid. † Glycera. ‡ Gravel in catch, near bottom. ‖ 1 *S. serratodendata*. ° 1 large polychæte, fair amount of gravel. ** 1 Autolytus. †† 1 Autolytus.

TABLE I—*continued.*

1930.	Leander sp. larvæ.	Pandalid larvæ.	Alphæid larvæ.	Crangonid larvæ.	Pontophilus spinosus larvæ.	Homarus vulgaris larvæ.	Phyllosoma larvæ.	Galatheid larvæ.	Galatheid post-larvæ.	Upogebia sp. larvæ.	Upogebia sp. post-larvæ.	Callianassa subterranea larvæ.	Axius styrhinchus larvæ.	Pagurid larvæ.	Pagurid glaucothoë larvæ.	Porcellana sp. zoea.	Porcellana sp. post-larvæ.	Ebalia sp. zoea.	Ebalia sp. megalopa.	Crab zoea.	Crab megalopa.	Squilla sp. larvæ.	Larval gastropods.	Echinospira larvæ.	Limacina retroversa.	Clione limacina.	Cephalopod young.	Young starfish.	Oikopleura.	Tornaria larvæ.	Fish eggs.	Total.
Feb. 4th	–	–	–	–	–	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	20	**17,787**
,, 12th	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	30	–	–	–	–	–	17	–	–	–	–	160	**19,280**
,, 19th	–	10	–	–	–	–	–	40	–	–	–	10	–	40	–	–	–	–	–	1,150	–	–	–	–	–	10	–	–	–	–	110	**13,792**
,, 26th	–	–	–	–	–	–	1	100	–	–	–	–	–	40	–	–	–	–	–	2,540	–	–	–	–	–	5	–	–	–	–	–	**3,844**
Mar. 5th	–	–	–	200	–	–	2	90	–	–	–	–	–	470	–	–	–	–	–	4,850	–	–	–	–	–	2	1	–	10	–	4,020	**11,888**
,, 12th	–	–	–	40	–	–	–	10	–	–	–	–	–	20	–	–	–	–	–	910	–	–	–	–	–	1	–	–	–	–	2,500	**4,041**
,, 19th	–	20	–	20	–	–	–	140	–	–	–	–	–	580	–	–	–	–	–	16,780	–	–	–	–	–	–	–	–	–	–	5,620	**23,177**
,, 27th	–	–	–	–	–	–	1	–	–	–	–	–	–	270	–	–	–	–	–	8,270	–	–	–	–	–	5	–	–	–	–	2,750	**13,799**
April 2nd	–	–	–	50	–	–	2	160	–	–	–	–	–	40	–	–	–	–	–	930	–	–	–	–	–	–	–	–	140	–	4,590	**5,987**
,, 11th	–	30	–	–	1	–	1	10	–	–	–	–	–	10	–	–	–	–	–	130	–	–	–	–	–	–	–	–	90	–	740	**2,445**
,, 16th	–	170	–	60	90	–	10	870	–	–	–	–	–	480	–	40	–	–	–	3,650	110	–	–	–	–	–	–	–	–	–	3,850	**26,945**
,, 24th	–	30	–	390	30	–	4	300	–	–	–	–	–	260	–	50	–	–	–	12,810	650	–	–	–	70	–	–	–	–	–	800	**26,419**
,, 29th	–	40	–	90	40	–	–	330	–	–	–	–	–	110	–	190	–	–	–	1,420	61*	–	–	–	–	–	–	–	100	–	900	**5,888**
May 7th	–	386	–	–	–	–	9	1,737	–	–	–	–	–	–	3	386	–	–	–	7,334	386	–	–	–	–	–	–	–	579	–	1,737	**335,784**
,, 15th	–	200	–	40	120	–	–	3,540	–	–	–	–	–	440	–	960	–	–	–	14,640	280	–	+	–	140	–	–	–	20	–	860	**53,302**
,, 22nd	–	390	–	80	30	–	32	2,890	–	10	–	–	–	540	–	810	–	–	–	8,430	550	–	+	10	90	–	–	–	–	–	190	**27,671**
June 10th	–	660	–	250	7	–	24	1,140	–	60	–	–	–	150	–	1,120	–	–	–	9,530	400	–	+	–	280	–	–	–	10	–	350	**19,291**
,, 19th	–	300	–	100	8	–	5	780	–	180	–	–	–	80	–	220	–	20	–	4,580	520	–	80	20	280	–	–	–	–	–	300	**16,696**
,, 26th	–	480	–	320	21	–	41	3,020	–	440	–	–	–	860	–	880	–	940	–	8,440	140	–	80	–	4,320	–	–	–	–	440	960	**37,052**
July 4th	2	80	–	20	–	–	3	380	–	–	–	–	–	140	40	800	–	–	–	1,540	180	–	40	–	600	–	1	–	–	120	1,120	**13,830**
,, 9th	31	300	–	120	1	–	–	2,130	–	1,170	–	90	–	1,560	60	300	–	420	–	13,410	900	–	300	–	1,710	–	1	–	–	4,890	120	**96,342**
,, 14th	35	510	–	240	–	–	78	2,730	–	1,980	30	60	–	360	–	3,060	120	780	–	12,900	1,230	–	+	–	23,310	–	1	–	–	3,030	180	**105,037**
,, 23rd	3	1,020	–	390	–	–	70	3,390	30	360	–	60	–	1,710	60	1,740	120	360	570	17,220	2,280	–	+	–	8,790	–	1	–	–	720	30	**85,176**
,, 29th	–	780	–	90	–	–	1	540	30	930	1	120	12	750	–	2,550	–	30	90	4,920	1,500	–	+	–	2,250	–	4	–	30	930	30	**48,554**

Aug. 7th	11	330	–	120	–	–	5	2,160	30	3,210	–	1,740	–	1,230	–	810	–	180	30	8,880	1,650	–	+	–	660	–	3	60	–	210	120	**76,736**
,, 14th	1	600	–	80	–	1	1	980	–	1,180	5	360	3	1,080	1	2,840	100	20	40	2,620	980	–	1	–	480	–	9	42	–	–	60	**56,799**
,, 21st	1	160	–	80	–	–	–	80	–	140	5	300	–	80	21	440	–	–	–	580	400	–	40	–	–	–	4	11	–	–	–	**36,010**
,, 28th	1	100	12	60	–	–	5	140	–	1,160	–	860	–	360	–	940	120	–	40	3,220	680	30	–	–	–	–	3	45	–	–	–	**26,397**
Sept. 3rd	2	320	23	160	–	1	2	60	20	80	–	1,380	–	380	2	120	60	80	100	1,840	540	5	40	–	–	–	–	90	–	20	–	**30,658**
,, 11th	–	40	–	–	–	–	–	60	–	40	–	280	–	160	41	140	–	–	20	360	100	–	–	–	–	–	1	51	–	–	20	**21,279**
,, 16th	10	30	2	10	–	–	–	20	–	30	–	160	–	60	–	–	–	–	–	470	40	10	–	–	–	–	–	167	20	–	10	**7,587**
,, 24th	1	–	–	–	–	–	–	–	–	50	–	20	–	10	–	300	–	–	–	900	80	2	–	–	–	–	2	2	20	–	10	**7,369**
Oct. 1st	1	–	2	–	–	–	–	–	–	–	–	–	–	50	–	60	–	–	–	20	30	1	–	–	–	–	–	3	100	–	–	**2,196**
,, 7th	–	10	1	–	–	–	–	10	–	20	–	–	–	20	–	170	–	–	–	250	40	–	–	–	–	–	1	62	80	–	–	**2,930**
,, 14th	–	–	2	–	–	–	–	–	–	50	–	–	1	10	–	210	–	–	–	210	20	–	–	–	–	–	1	–	10	–	10	**6,316**
,, 16th	–	1	7	–	–	–	–	–	–	190	–	–	–	60	–	440	–	–	–	440	20	–	–	–	–	–	–	–	240	–	–	**4,044**
Nov. 6th	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–	10	–	–	–	60	10	–	–	–	–	–	–	10	–	–		**2,528**
,, 13th	–	–	3	30	–	–	–	–	–	–	–	10	–	30	–	–	–	–	–	30	10	–	–	–	–	–	–	–	190	–	10	**1,832**
,, 20th	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	10	–	–	–	–	–	–	–	–	40	–	492†	**2,070**
,, 26th	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	70	10	–	–	–	–	–	–	–	–	–	160†	**1,180**
Dec. 3rd	–	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	1	–	–	40	–	–	–	–	–	–	–	–	20	–	20	**3,274**
,, 10th	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	–	–	–	40	–	190	**2,185**
,, 17th	–	–	–	10	–	–	–	–	–	–	–	–	–	120	–	–	–	–	–	40	20	–	–	–	–	–	–	–	100	–	20	**1,958**
,, 22nd	–	–	–	10	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	40	–	–	–	–	–	–	–	–	70	–	70	**708**
1931.																																
Jan. 1st	–	–	–	–	–	–	–	10	–	–	–	–	–	90	–	–	–	–	–	90	20	–	–	–	–	–	–	–	60	–	90	**1,342**
,, 5th	–	–	–	1	–	–	–	–	–	–	–	–	–	70	–	–	–	–	–	210	10	–	–	–	–	–	–	–	40	–	100	**1,220**
,, 15th	–	10	–	–	–	–	–	–	–	–	–	–	–	80	–	–	–	–	–	80	10	–	–	–	–	–	–	–	590	–	1,270	**6,704**
,, 22nd	–	10	–	–	–	–	–	50	–	–	–	–	–	30	–	–	–	–	–	140	–	–	–	–	–	–	–	–	110	–	1,300	**2,431**
,, 26th	–	–	–	–	–	–	–	–	–	–	–	–	–	50	–	–	–	–	–	80	–	–	–	–	–	–	–	–	70	–	640	**1,134**
Feb. 6th	–	–	–	10	–	–	–	90	–	10	–	–	–	20	–	–	–	–	–	370	–	–	–	–	–	–	–	–	50	–	910	**1,563**
,, 12th	–	–	–	–	–	–	–	90	–	–	–	–	–	90	–	–	–	–	–	240	–	–	–	–	–	–	–	–	50	–	530	**1,182**
,, 20th	–	–	–	–	20	–	–	810	–	–	–	–	–	260	–	–	–	–	–	6,840	30	–	–	–	–	–	–	–	110	–	7,140	**16,973**
,, 23rd	–	30	–	10	10	–	–	750	–	–	–	–	–	710	–	–	–	–	–	7,170	90	–	–	–	–	–	–	–	–	–	7,090	**17,354**
,, 26th	–	–	–	20	10	–	–	90	–	–	–	–	–	40	–	–	–	–	–	4,840	10	–	–	–	–	–	–	–	–	–	780	**11,949**
April 1st	–	80	–	20	–	–	–	80	–	–	–	–	–	600	–	–	–	–	–	14,480	20	–	–	–	–	–	–	140	–	–	80	**18,368**
,, 16th	–	140	–	60	–	–	–	200	–	20	–	20	–	1,460	–	360	–	–	–	11,060	140	–	–	–	–	–	–	–	–	–	1,040	**31,683**

* 1 small ♂ pea crab.

† Pilchard.

On the Biology of *Calanus finmarchicus*. I. Reproduction and Seasonal Distribution in the Clyde Sea-Area during 1932.

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With 4 Figures in the Text and Plates I and II.

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INTRODUCTION.

THE problems concerned with the breeding of *Calanus finmarchicus* have been dealt with by numerous workers, mainly during the last twenty years. Taken as a whole the results show remarkable uniformity if the differences in methods of sampling and in the geographical regions over which the work has been spread, are taken into account.

The two points which stand out on reviewing this work are firstly, that breeding occurs in spring and summer and secondly, that during the winter the species is represented by its fourth and fifth copepodite stages, chiefly the latter (Farran, 1927, p. 142).

Work in the Clyde Sea-Area was undertaken to discover to what extent this area was in agreement with other regions of northern temperate waters and to obtain more detailed information on the number of breeding periods, the time taken for development, and other related facts. This work was an extension of the programme carried out by Marshall and Orr in 1931 (Ann. Rep. Scot. Mar. Biol. Assoc., 1930–31).

This area with its semi-enclosed lochs appears to be particularly suitable for such work since it is separated from the waters of the Irish Sea and the Atlantic by a comparatively shallow platform. Unfortunately, little is known about the currents entering the Clyde Sea-Area, but those drift-bottle experiments which have been carried out by Cunningham (1907) of the Irish Fisheries Board lend support to the view that no deep-water currents enter the area. (Other drift-bottle experiments affecting this area have dealt only with surface drift.) The lochs of this area are, in most cases, still more completely cut off from outside waters by bars (Mill, 1889–91 ; Marshall and Orr, 1927) of shallow depth across their mouths.

It is felt that movements of surface waters will not affect the population to any great extent and will in any case be dependent upon weather conditions.

It seems certain then, especially in the lochs, that any changes in the numbers of Calanus will be due to factors operating within the locality.

STATIONS AND METHODS.

Four stations were selected within the area for investigation and comparison (see Map, Text-Figure 1). Station I was situated over the deepest part of the channel between the south end of Bute (Garroch Head) and the Little Cumbrae. This station had an average depth of 113 metres, and was taken as typical of the open waters of the Clyde Sea-Area. Station II was in the channel which runs in a north-westerly direction between Arran and Bute, ending in a " deep " of about 200 metres at the mouth of Loch Fyne. The average depth of this station, which was midway between the north of Arran (The Cock of Arran) and Inchmarnock, was 151 metres. Station II, also, was assumed to be typical of the open waters of this region and acted as a check upon Station I.

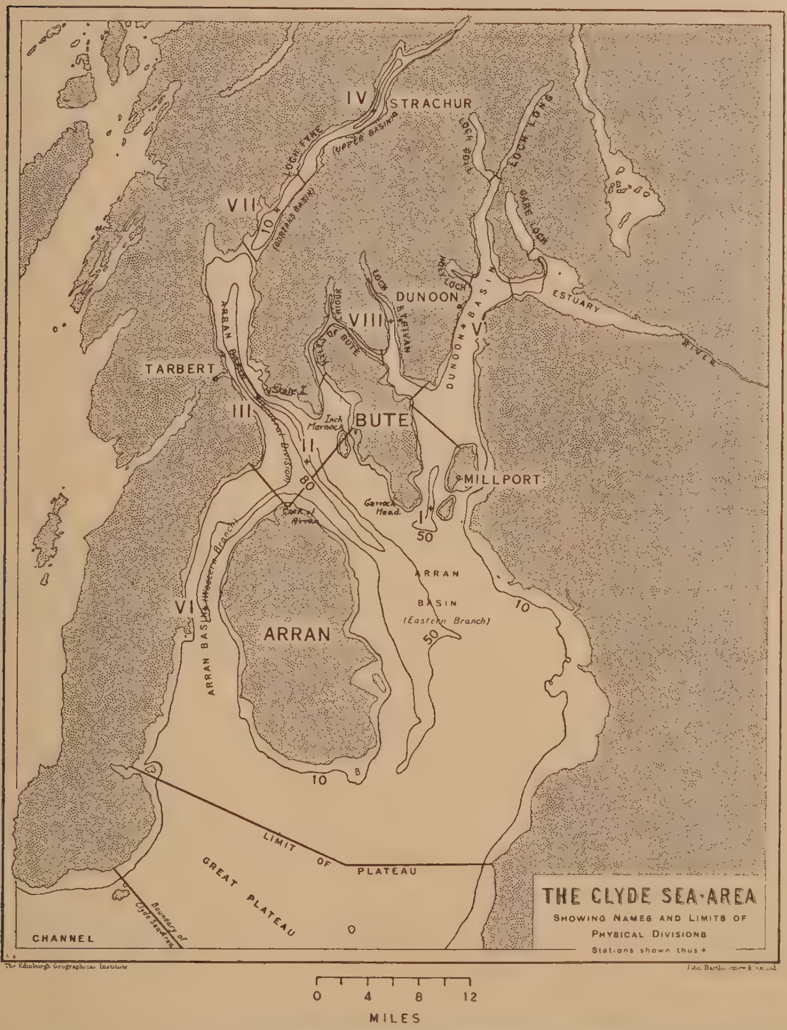
Station III was situated in the vicinity of the " deep " at the mouth of Loch Fyne, off Skate Island. The catches from this station were not counted, but rough observations were made to check the possibility of the loch forming a breeding ground whence Calanus might spread to the rest of the area, since it was known from previous work in this area that Calanus was abundant there at times when it was very scarce elsewhere.

Station IV was nine or ten miles from the head of Loch Fyne, in the deepest part of the loch, off Strachur. Upper Loch Fyne is separated from the rest of the area by two bars which divide the loch into three basins, Strachur being in the innermost. The average depth of the hauls was 130 metres.

It was hoped that these stations would give a comparison between the loch and the open waters, and that some light might be thrown on the reason for the large numbers of Calanus present here when they were scarce elsewhere.

Three other stations were selected, one off Dunoon (Station V), a second in the Kilbrennan Sound (Station VI), and the third about half-way up Loch Fyne in the middle, or Gortan's Basin (Station VII), and these were visited and hauls taken at quarterly intervals to provide a further check upon the validity of the regular stations.

Vertical hauls were taken at each of the stations with a modified form of the Standard Net described by Ostenfeld and Jespersen (1924). The cylindrical part of the net was made of canvas instead of netting and the conical part of fine-meshed bolting-silk (77 strands in 1 cm.). An ordinary townet bucket was used. A hand winch was used for hauling the net, the


IV
STRACHUR
LOCH FYNE
(UPPER BASIN)
(LOWER BASIN)
LOCH ECK
LOCH LONG
GARE LOCH
VII
10
HOLY LOCH
DUNOON
ESTUARY
RIVER
LOCH RIDDON
LOCH STRIVEN
VIII
KYLES OF BUTE
DUNOON BASIN
V
TARBERT
ARRAN BASIN
Skate I.
III
Inch Marnock
BUTE
II
80
MILLPORT
Garroch Head
Cock of Arran
I
50
ARRAN BASIN (Eastern Branch)
50
10
VI
ARRAN BASIN (Western Branch)
ARRAN
10
LIMIT OF PLATEAU
GREAT PLATEAU
0
CHANNEL
Boundary of Clyde Sea-Area
THE CLYDE SEA-AREA
SHOWING NAMES AND LIMITS OF PHYSICAL DIVISIONS
Stations shown thus +
The Edinburgh Geographical Institute
John Bartholomew & Son Ltd.
0 4 8 12
MILES

TEXT-FIG. 1.—Map of the Clyde Sea-Area showing positions of Stations. Depth contours are shown for 10, 50, and 80 fathoms.

rate at first being kept as nearly as possible to half a metre per second, which approximates to that given by Ostenfeld and Jespersen. Later, as the meshes of the net became smaller with use, allowance was made for the reduced filtration and more time was taken for hauling.

The first hauls were taken on September 3rd, 1931, and continued at approximately fortnightly intervals until September 5th, 1932, a final haul being made on October 30th. At Station I extra hauls were taken when possible from March to June, making the intervals between hauls approximately a week. At the time of taking each haul notes were made of the depth of the haul, time of day, and of the time taken to haul the net from the bottom to the surface (Table I). The condition of sea and sky, and approximate force and direction of the wind were also noted.

Each station was visited at approximately the same time of day throughout the year. In a few cases, owing to weather conditions or other factors, this was not possible.

The catches were preserved in 5% formalin at the time of taking and later sorted and counted in the laboratory. For counting, Russell's modification of Bogorov's counting tray was used and found very satisfactory. A description of this tray will be found in the Scientific Reports of the Great Barrier Reef Expedition, Vol. II, 2, 1931, p. 24. My thanks are due to Mr. F. S. Russell for procuring this tray for me.

All stages from ovum to adult were counted. It was considered that a count of 1,000 would give a representative sample of the number of different stages present in the catch. In some cases this necessitated taking an aliquot sample of the catch for counting. When this was done the method described by Russell (1925, p. 776) was used. Since the apparatus in use was not identical with that described by him, the method was checked by dividing a catch into ten parts and counting each. The error in sampling was found to be similar to that obtained by Russell (p. 775).

Before examining the results of this work there are one or two points to be borne in mind.

Allowance must be made for the error incurred in using single vertical hauls as the means of obtaining the catches. It has been shown by Gardiner (1931, p. 457) that in 145 hauls, two may be taken which will deviate from the mean by as much as 90% and that occasionally even greater deviation may be expected. He states, however, that variation in the speed of hauling and in the time of day at which the hauls are made does not cause appreciable errors and the conclusion is reached that "the main cause of variation in the size of the catch" is probably due to "lack of uniformity in the distribution of the organisms themselves" (p. 467).

In the course of this investigation over 130 hauls were made of which over 100 were counted and the possibility of "freak" hauls occurring must be taken into consideration. To safeguard as far as possible against the occurrence of such "freak" hauls Gardiner suggests that 5 hauls as a minimum should be taken at each station, since 4 out of 5 will probably confine the deviation to under 40% and "give a value which for all practical purposes may be considered the true one." As he points out this requires much time.

Another factor to be considered is the difficulty of identifying the different nauplius stages and of separating these and the ova from those of other copepods without taking too much time. In most cases this separation could only be done by means of measurements, which must always be approximate owing to the variation in size of the individuals of each particular stage. The ova and nauplii of Pseudocalanus closely resemble those of Calanus and even the difference in size is not marked thus early in the life history. The figures for the nauplii, therefore, must not be regarded as being as accurate as those for the copepodites.

The initial difficulty of identification of the nauplii of Calanus was overcome with the assistance of Dr. M. V. Lebour, to whom I am indebted for sending me specimens of such nauplii from the English Channel.

Variations in the depth from time to time at different stations has not been regarded as important and no allowance has been made for such variation.

It is with pleasure that I take this opportunity of expressing my thanks to my colleagues, Miss S. M. Marshall and Mr. A. P. Orr, for much practical assistance from time to time.

RESULTS.

In the charts, Plates I and II, will be seen the variation in the population of Calanus in this area from September, 1931, to September, 1932. The results obtained from each of the three stations counted are shown, expressed as total numbers in Plate I and as percentage composition in Plate II. Details of catches at all stations will be found in Tables II, III, IV, and V.

Owing to the considerable variation in total numbers it was impossible in Plate I to represent the individual stages separately throughout, so the Calanus were divided into four groups, ova, nauplii, copepodite stages, and adults. In the case of the percentage chart it was found necessary to group only the nauplii (I–VI) and the copepodite Stages I–III, each of the others being given individual representation.

On examining the total numbers curve for Station I (Garroch Head) it will be seen that numbers were low in September and decreased further through the autumn and early winter and it was not until the end of March that an increase occurred. This was of short duration. Numbers then increased suddenly at the end of April and through May, thereafter falling away steadily to reach a constant level in August. A final haul taken at the end of October showed little change.

Turning now to the percentage chart (Plate II) for this station it will be seen that Stage V copepodites formed the bulk of the catch through the autumn and early winter. During October and November ova, nauplii, and young copepodites formed a large percentage, but were very small in actual numbers and not sufficient to make any marked increase in total numbers. At the end of December the Stage V copepodites began to moult into adults, the maximum percentage of males being attained at the beginning of February, the largest actual number having occurred a fortnight earlier. Females attained their maximum number and percentage on February 22nd.

As will be seen from Table II the ova and nauplii found in January were relatively unimportant though representing a fair proportion on the percentage chart. There were no ova or nauplii on February 8th, but on 22nd 84 ova were found, representing 57% of the catch, females amounting to 37%. From this time onwards there followed a regular sequence of ova, nauplii, copepodites, and adults.

The adults which had moulted from the autumn-winter stock of Stage V copepodites died out early in March to be replaced shortly after by their own offspring which, liberated as ova soon after February 8th, appeared as adults soon after March 7th. Through April and May these in turn produced ova which began to reach maturity in May and June. From the middle of May until the end of June this second brood liberated eggs which grew to maturity, the later ones remaining as Stage V copepodites. Further successive small broods of ova in July and August added to the number of Stages IV and V copepodites which were to carry the stock over the autumn and early winter.

Total numbers at Station II (Cock of Arran) in September, 1931, were over 2,000, i.e. higher than those of Station I, and maintained a fairly high average (over 3,000) until the end of November, by which time a considerable and real fall off in numbers was observable, 1,000 being reached on only one occasion after that time until breeding had started in the spring.

On May 2nd numbers increased to over 40,000 from having been under 500 on April 18th, to be followed by as sudden a fall to below 4,000 a fortnight later. From this date numbers showed a gradual fall to the end of June, followed by a gradual rise to the end of September, maintaining an average of just over 2,000 for the period. The average had fallen to under 1,000 by the end of October.

It will be seen from Plate II that, as at Station I, through the autumn and early winter nearly 90% of the Calanus present were Stage V copepodites with a small percentage of Stage IV and a very few adults. Moulting of these Stage V copepodites started at the same time as at Station I, both males and females attaining their greatest numbers on February 8th.

Ova appeared shortly after January 25th and from February 8th until 22nd increased rapidly in number, falling off again to March 7th. These ova appeared as adults from March 7th until early in May. On April 18th an increase in the number of ova was again noticeable which was followed by the extraordinary increase of May 2nd, when over 34,000 ova and about 5,000 nauplii were estimated to be present. These as quickly disappeared, leaving only about 900 ova, 1,300 nauplii, and 1,500 copepodites.

For the next two months the number of ova was fairly constant, but the number of nauplii and copepodites fell off so that in the latter half of June a third noticeable increase is represented in the percentage chart for this station. Through July and August the number of Stage V copepodites moulting into adults decreased, resulting in an increase in the number of copepodites to form, as at Station I, the autumn-winter stock.

At Station IV (Strachur) the numbers of Calanus (mainly Stage V copepodites) averaged 10,000 for the first six weeks of this investigation. They then fell away steadily from November to March, by which time the survivors had all become adults, which as at Stations I and II first appeared at the end of December and attained maximum numbers on February 8th; the males far outnumbered the females all the time (see Table IV).

It is impossible to follow the sequence of events at Stations V, VI, and VII, where hauls were taken only quarterly. The figures for these stations, however (Table V), show no striking disagreement with those for other stations at the times when these hauls were taken, except that in winter numbers were usually much lower.

Discussion.

The most striking features in the chart showing total numbers (Plate I) are: firstly, a fairly high number of Calanus present at the beginning of the autumn, gradually falling away to a minimal value, well under 500 in every case, at the time when reproduction is starting in the spring; secondly, the coincidence of large catches from the two stations in open waters (I and II) on May 2nd; thirdly, the disappearance of this sudden increase; and fourthly, the smaller number of Calanus present in September, 1932, compared with the same time in the previous year.

Noticeable features of the percentage chart (Plate II) are the homogeneity of the Calanus population during the autumn and winter at two stations in particular (II and IV); the appearance of three successive and well marked breeding periods at all three stations, coincident at I and II and the first slightly delayed and overlapping the second at Station IV; and the accumulation of copepodites of Stages IV and V, particularly the latter, at all stations after the middle of July.

This minimum, occurring towards the end of winter, seems to be of general occurrence and has been found by several investigators working on Calanus. Farran (1927, p. 142) investigating the same problem off the south-west coast of Ireland found a minimum in March. Ruud (1929, p. 78) studying the copepod population off the coast of Norway also found the number of Calanus to be at a minimal value in March and the recent work of Sömme (1933, p. 32) confirms this. At Station I in this area Calanus were very scarce from November to the beginning of March. At Station II low numbers were recorded from January until March, the actual minimum falling early in the latter month; but at Station IV numbers did not reach low values until the beginning of March and the minimum was delayed until April, by which time numbers were increasing at the other stations.

The low numbers found by Sömme at the end of March are ascribed to a definite migration of Calanus towards the surface early in March, after which they were carried away by surface currents. This can scarcely be the cause in the Clyde Sea-Area since it has been shown that currents can play little part in such an enclosed area. Moreover, any outward migration from Loch Fyne would have been detected at Stations II and III as explained below.

Natural mortality, possibly directly connected with food supply, will account for the steady decrease in numbers through the course of the winter leaving comparatively few females to produce the first brood which is, consequently, small in numbers compared with later broods.

Farran (1927, p. 137) found that in January males were more abundant than females and that in the following month females were in excess. This was apparent at Stations I and II though numbers were low; at Station IV males were more numerous than females right through this period, and it was not until April 18th, when the new brood had developed, that females noticeably outnumbered males.

The result, then, of this gradual moulting of the autumn-winter stock of Stage V copepodites was the production of a brood of ova, small in numbers compared with later broods, which gave rise to a new brood of adults, mainly females. These appeared through March and April (see Plate II). It was these adults which produced the extraordinary increase at Stations I and II at the beginning of May, to which reference will be made later.

We must here take into consideration the probable life of a single

Calanus ; the time taken for the development of the ovum to the adult ; and the probable number of ova produced by one female.

From an inspection of the percentage chart (Plate II) and Table III showing numbers throughout the year at Station II, it will be seen that by March 7th males, females, and Stage V copepodites of the autumn-winter stock have disappeared completely from the catch, their places being taken by younger stages which they have themselves produced. This clearly indicates that all the fifth copepodites of the autumn-winter stock moult or die at this time and that those which reach maturity, having spawned, die also. Gran (Paulsen, 1906) and Damas (1905) concluded that the individuals normally died after breeding.

This limits the life of a Calanus to one year, but in all probability it is much less. On examining the column of numbers for females for Station I (Table II) it will be seen that from December 29th to February 22nd they increase from 1 to 55, falling away rapidly to 1 at March 7th. This is followed by a sudden increase to 62 by March 21st, rising gradually to 99 on April 18th and falling away again a fortnight later to 47. This is, in turn, followed by a sudden increase to 104, rising to 757 on May 23rd and falling with fluctuations to 15 on June 13th. Once more this is followed by a sudden rise to 205 on June 27th with a fall to the end of July and a sudden drop thence to August 8th, after which the numbers remain steadily low. A similar state of affairs is observable at the two other stations.

The conclusion is that though the adult life of the females from the autumn-winter stock may be nine weeks, for succeeding broods it is not more than 6 or 7 weeks.

The results from Station I (Plate II) show that from March 7th until 21st females increased rapidly (1 on 7th to 62 on 21st), corresponding with the increase in the number of ova from February 8th to 22nd (0 on 8th to 84 on 22nd). This indicates a maximum period of 28 days for the development of the ova to adults at this time of year. The ova and nauplii present before February 8th were insignificant in number and may be neglected.

Subsequent experimental work carried out in the laboratory (jointly with Miss S. M. Marshall) confirmed the view that four weeks was the maximum time required for the ova to reach maturity.

Calanus of different stages were kept each in a separate beaker, the sea-water of which was changed daily and the Calanus examined. The temperature was kept as close as possible to that of the sea at the time (June, July, and August), by standing the beakers in shallow tanks through which sea-water was circulating. It was assumed that each Calanus would find sufficient food for its daily requirements in 250 c.c. of sea-water. Each specimen was kept until it had moulted at least twice so that the interval between each successive stage in its development could be fixed. Females were kept and the time noted from the shedding of the ova to the appearance of nauplii. It was difficult to distinguish the different nauplii while living, so the time taken to pass through the nauplius stages was taken from the shedding of the ova to the appearance of the first copepodite. The minimum time was eleven days. Each of the successive moults up to Stage V occurred at minimal intervals of 3 days, and the shortest interval between the Stage V copepodite and the adult was 4 days. It will be seen that when the shortest intervals are added together 27 days are required for the complete development from the egg to the adult.

Ruud (1929) found that in the Norwegian Sea Calanus took about 3 months for its entire development. Lebour (1916) states: "Nauplii first appeared between the 17th and 24th of April, and on May 19th Stage V was taken from the jar, having taken certainly less than two months to grow from the egg to this stage." This shows close agreement with the results obtained in this region, and it must be remembered that the slower development in the Norwegian Sea is probably correlated with a lower temperature.

We have now two and a half months as the probable life of a single Calanus during the active breeding periods of spring and summer; one month in which to reach maturity and six weeks of adult life. But the Calanus produced towards the end of the breeding season will live through the autumn and winter until early the next spring, with a life of 5 or 6 months.

There seems to be no record of the number of ova produced by one female Calanus, neither has it been possible to obtain this information experimentally. Referring to the figures in Tables II, III, and IV and correlating the number of females on any particular date with the number of eggs on the same date we find a variation of from 1 to 120 eggs per female. It is probable that the number of eggs liberated by any one female is from 60 to 70, with larger numbers occurring occasionally. It seems possible, also, from observations on the copepod *Euchæta norvegica* (as yet unpublished) that each female can produce more than one brood of ova.

Reference has been made to the striking increase in the number of Calanus which was found on May 2nd. On this date at both outside stations (I and II) extraordinarily large catches of Calanus were obtained,

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EXPLANATION OF PLATES.

PLATE I.—Chart showing the changes in total numbers and composition of the population of *Calanus finmarchicus* at three positions in the Clyde Sea-Area for one year.

PLATE II.—Chart showing the changes in the percentage composition of the population of *Calanus finmarchicus* at three positions in the Clyde Sea-Area for one year.

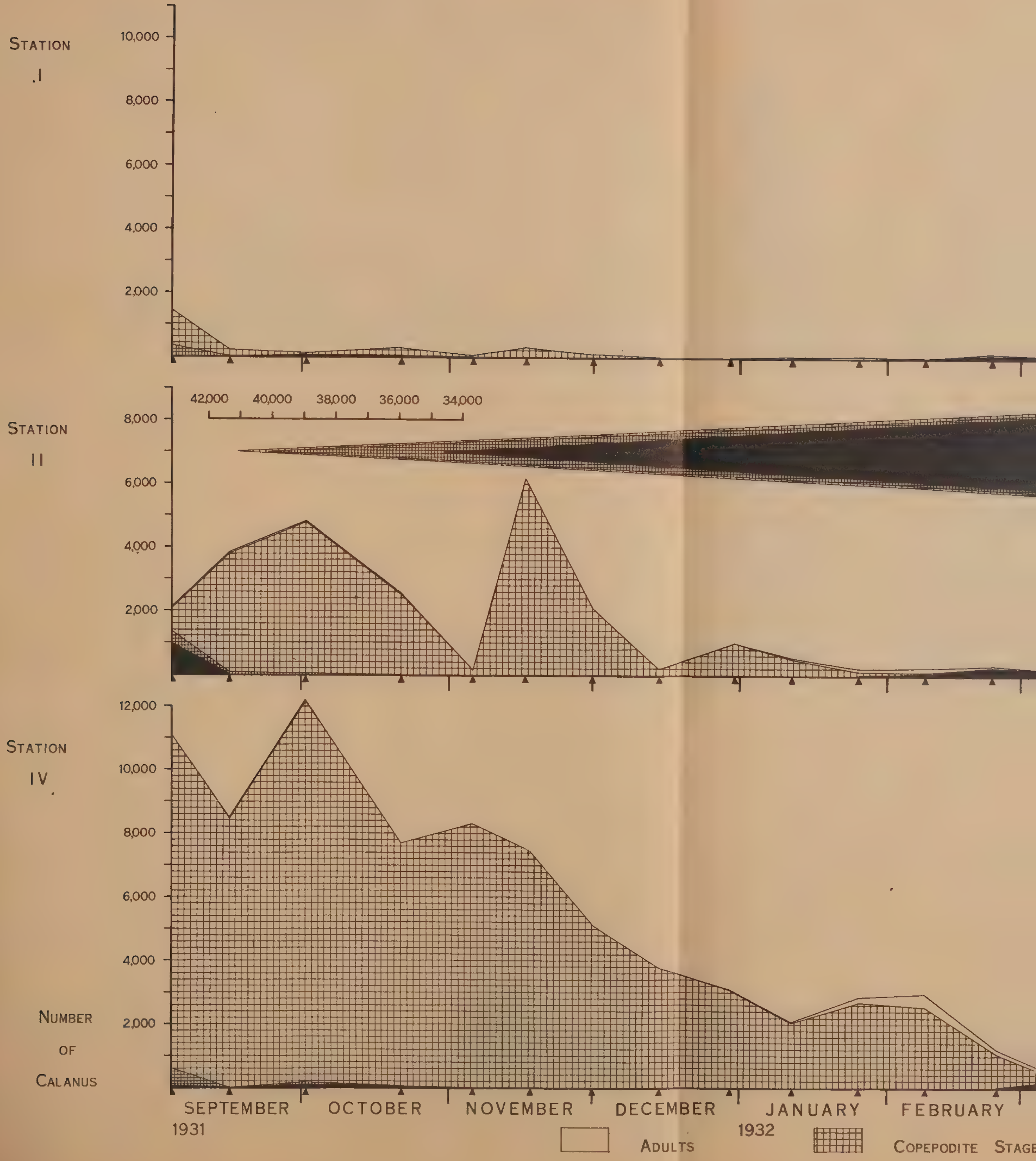
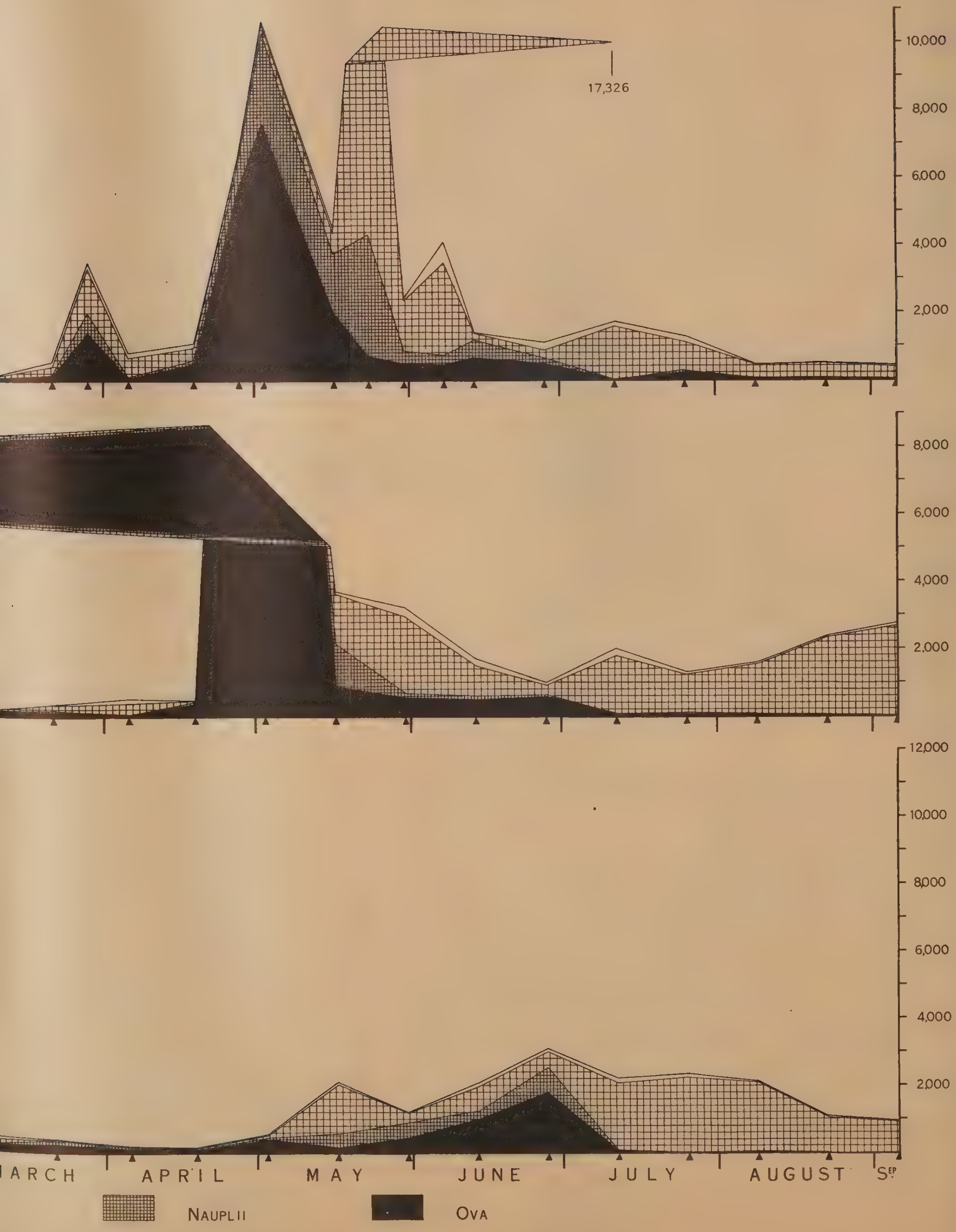

Station I
10,000
8,000
6,000
4,000
2,000
Station II
42,000
40,000
38,000
36,000
34,000
8,000
6,000
4,000
2,000
Station IV
12,000
10,000
8,000
6,000
4,000
2,000
Number of Calanus
September
1931
October
November
December
January
1932
February
Adults
Copepodite Stage

PLATE I.


10,000
8,000
6,000
4,000
2,000
17,326
8,000
6,000
4,000
2,000
12,000
10,000
8,000
6,000
4,000
2,000
ARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEP
Nauplii
Ova

Journ. Mar. Biol. Assoc. N.S. XIX—1.

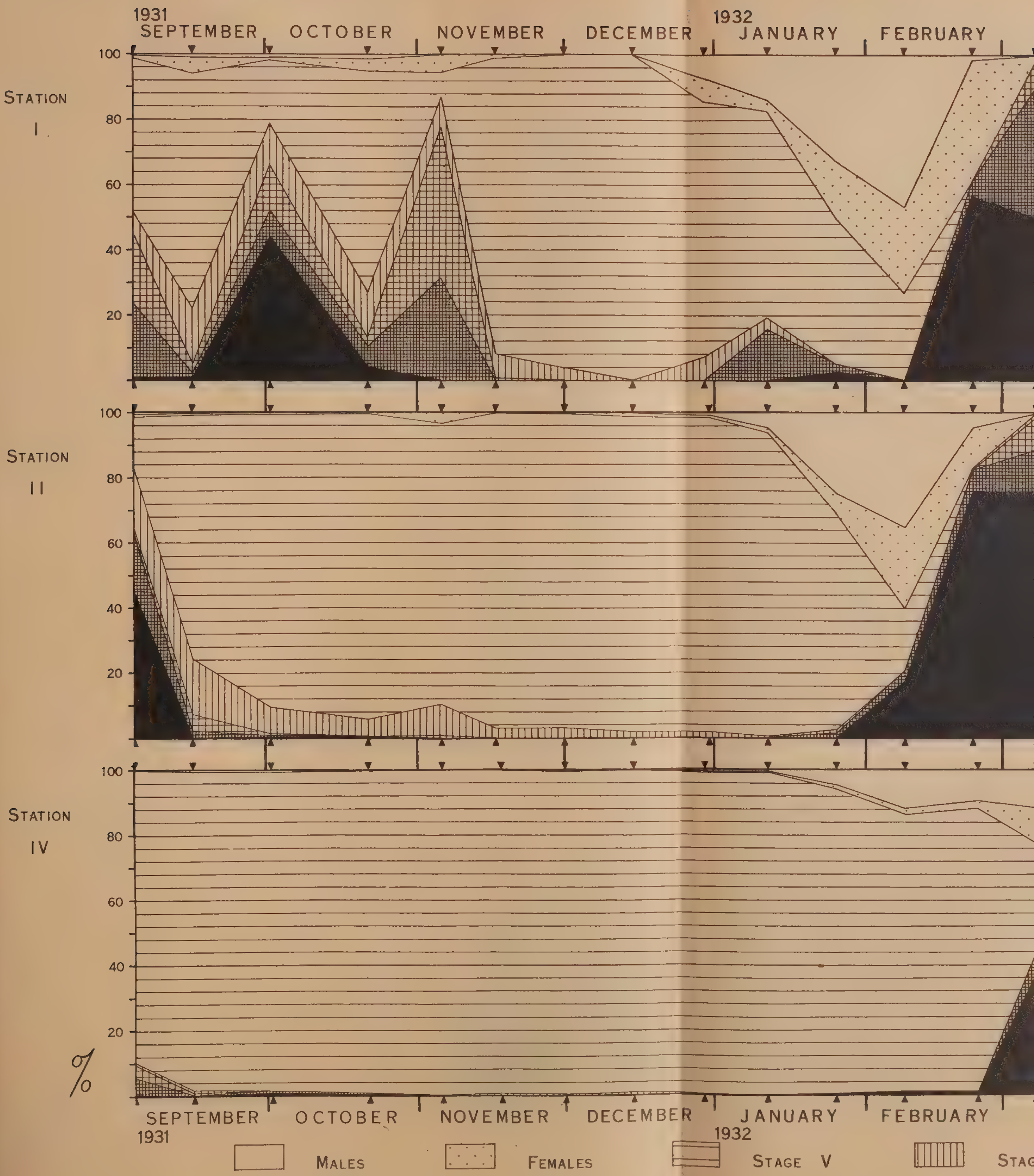
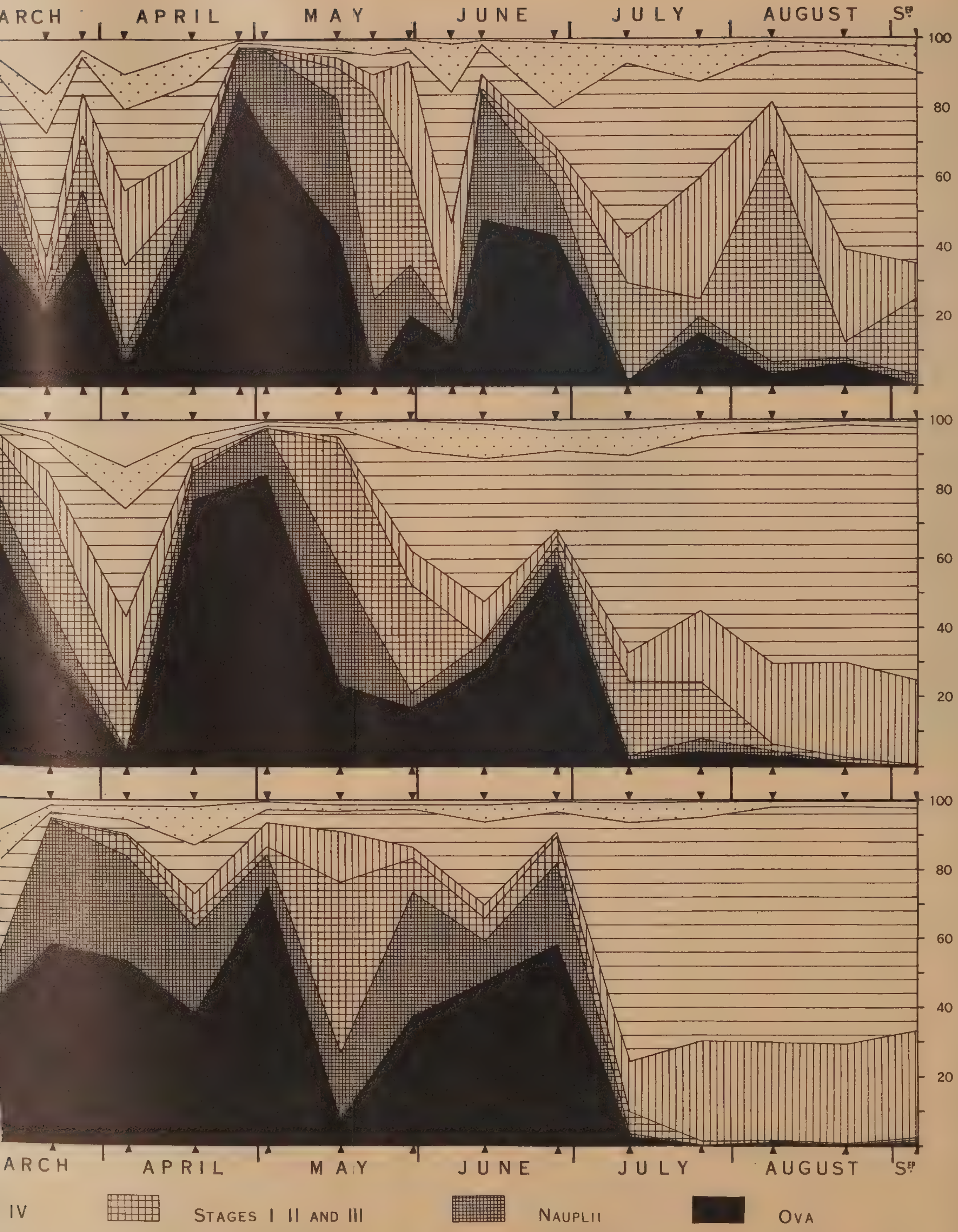


PLATE II.


ARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEP
100
80
60
40
20
IV
Stages I II and III
Nauplii
Ova

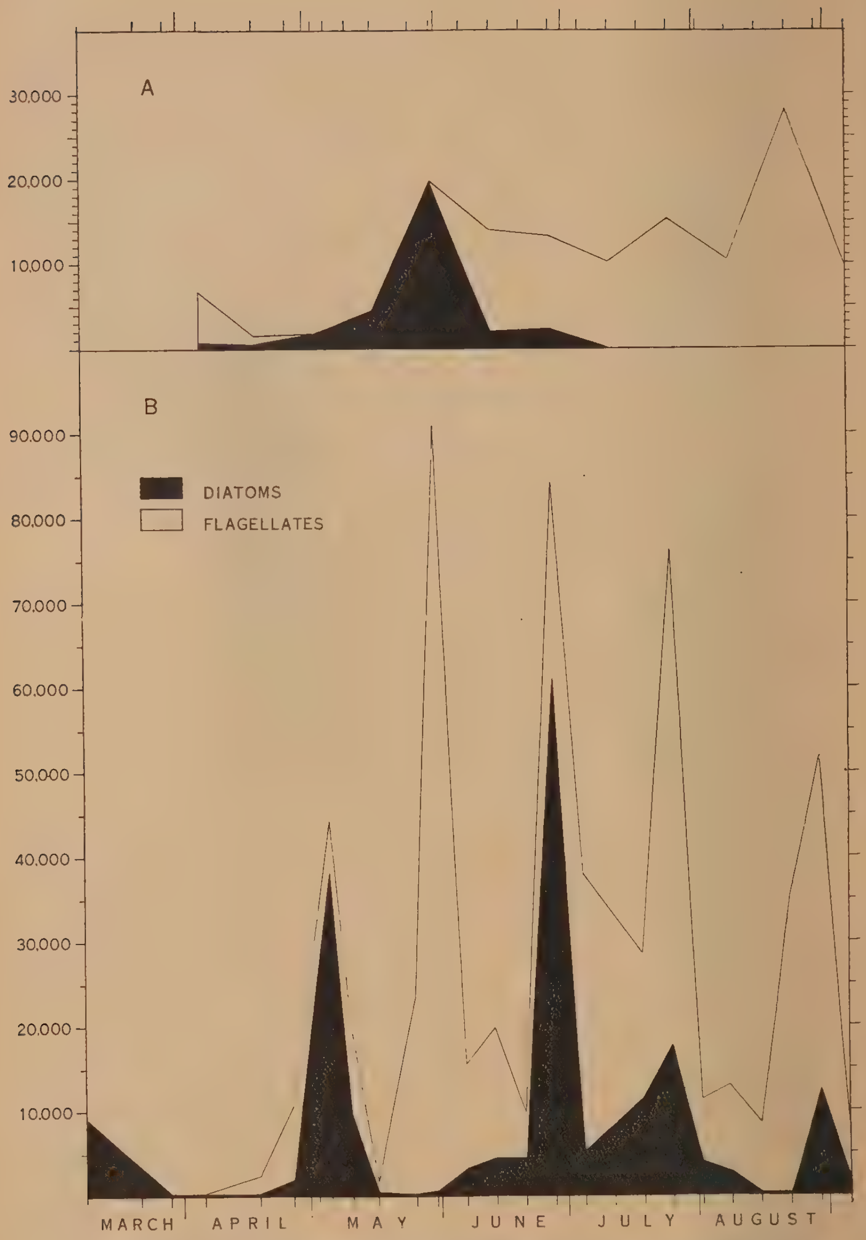
numbering over 10,000 at Station I and over 41,000 at Station II. Three weeks later another large catch (17,326) was obtained at Station I. In the first two cases this was due to a very large increase in the number of ova (with a ratio of not more than 70 per female) and an increased number of nauplii derived from these ova. Copepodite stages and adults, though present in numbers larger than usual, formed only a small percentage of the catch. On the second occasion of a large catch (May 23rd at Station I) copepodite stages formed the mass of the catch, Stages I, II and III being most abundant. These must have arisen from the ova liberated between May 2nd and 16th (about 9th) and the older copepodites would have been ova about May 2nd, and being older would have suffered more from natural mortality, the rate of which is high (p. 89).

Taking into account the length of life of the ovum as such and the time passed by Calanus in its nauplius stages, it is possible to say that, with one exception, at no time in the year were more copepodites found than could have been produced from the ova or nauplii present the requisite length of time before. The following hypothetical case may make this clear. If 10,000 ova were present on a certain date and 20,000 Stage II copepodites were found a fortnight later it might be argued that so many copepodites could not arise from so few ova and that, therefore, immigration must have occurred from some other locality where reproduction was in progress. It must be remembered, however, that whereas the ova remain as such for not more than 24 hours (Grobben, 1881) the copepodites remain in each stage for 3 days, and the effect will be an accumulation of copepodites. These will, of course, be subject to mortality.

The one exception referred to above occurred at Station I on May 16th when too few nauplii were present to produce the copepodites of May 23rd. This catch will have to be accepted as a "freak," since the number of ova present early in May was ample to produce the copepodites of 23rd.

At both stations the enormous increase found on May 2nd was of a temporary nature and died away as quickly as it had risen. This points to a very large mortality possibly correlated with the food supply. Farran (1927, p. 139) found reproduction was occurring generally in April and May, at which time numbers rose to ten times what they had been a few months before. Bigelow (1926, p. 168) records similar sudden increases in the number of Calanus in the Gulf of Maine during May.

Whereas Farran found a gradual decline in the numbers of Calanus subsequent to the increase in April and May, at both stations at which the decline occurred in this area it was sudden. Reference to the work of Marshall and Orr (1927, 1930) will show that the number of diatoms present during the spring increase of 1928 was over 5,000 cells per c.c. for some time and was over 12,500 cells per c.c. for a few days. Similar numbers were found in 1926 and 1927.



Text-Fig. 2.—Chart showing numbers of diatoms and of flagellates in 20 c.c. samples from the surface, A at Strachur and B at Keppel, from March until September, 1932. Other micro-organisms were negligible.

Text-Figure 2 shows the variation in the number of diatoms and in other microplankton at Keppel and at Strachur from March to September, 1932. I am indebted to Miss S. M. Marshall for the information expressed in this figure. It will be seen that though diatoms were spasmodically abundant during the spring and summer, on the whole numbers did not once reach those attained by the phytoplankton in the course of an ordinary spring increase and were, on the average, low for the whole season. The highest value reached at Keppel in 1932 was 3,000 cells per c.c. in June, and the spring increase figures were only 2,000 cells per c.c. It is possible, therefore, that under normal conditions the decline would have been as gradual as that found by Farran, and that the number present in the autumn of 1932 would have been similar to that of 1931.

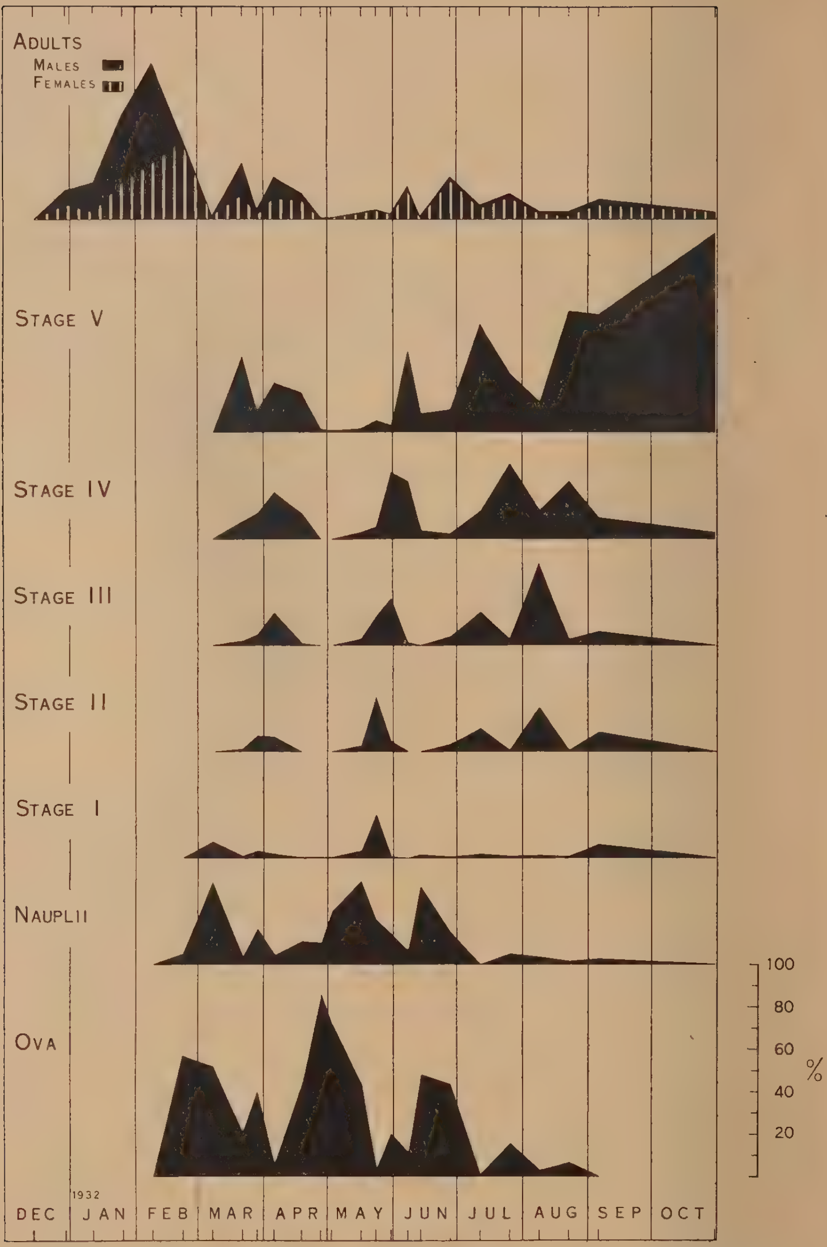
At Strachur (Station IV) diatoms were even less abundant (Text-Figure 2, A) and the Calanus in September, 1932, numbered about 1,000 compared with 10,000 in September of the previous year.

It has already been seen that as autumn approaches development is arrested and the Calanus remain as Stage V copepodites, mixed with a number of Stage IV and a very few adults.

The next point which arises is the appearance of three well defined breeding periods on the percentage composition chart (Plate II). This becomes more marked if the percentage composition of the catch during the reproductive season is separated into different stages and each is graphed individually (Text-Figures 3 and 4 ; in these figures certain details present in the chart, Plate II, which would only tend to confuse the issue, have been left out.) Here is plainly marked the succession of stages from ovum to adult in three successive breeding periods followed by the subsidiary ones at the end of the summer. This is not so obvious at Station IV where the results are confused by the large initial lag and a subsequent overlapping of the first two breeding periods.

The results from Station II (Text-Figure 4) suggest an almost diagrammatic accuracy. Each maximum of females is followed by a maximum of ova, and this maximum can be followed through each stage to adults, which attain their maximum at a month after the maximum of ova, and so on through the summer.

The difficulty which arises is to explain why there should be such a long interval between any maximum of females and the following maximum of ova, the latter actually coinciding with a minimum of females. It appears that the Calanus, having moulted into adults, require from three weeks to one month for maturation of the reproductive organs and for the transference of the spermatophores to the females, and that meanwhile they are subject to a high rate of mortality so that by the time that sexual maturity is reached comparatively few females remain. Thus the egg peak would coincide with the female minimum. The number of



TEXT-FIG. 3.—Diagram illustrating the succession of breeding periods at Station I (Garroch Head). Copepodite Stages IV and V occurring prior to February 22nd and ova and nauplii prior to February 8th have been omitted.

females then rises again a month later when these ova have completed their development.

This explanation appears satisfactory in its general application. If, however, we examine the curve for Station I (Plate II and Text-Figure 3) we find a number of inconsistencies with this hypothesis. Firstly, a secondary peak of ova is present at the end of the first breeding period. If this were the result of an almost immediate liberation of ova from these females which reached maturity on March 21st, it would leave only one week for the maturation of the reproductive organs and fertilisation of the females. This would appear to be too short, and, moreover, would result in continuous breeding throughout the reproductive season and a more or less constant representation of all stages throughout this period.

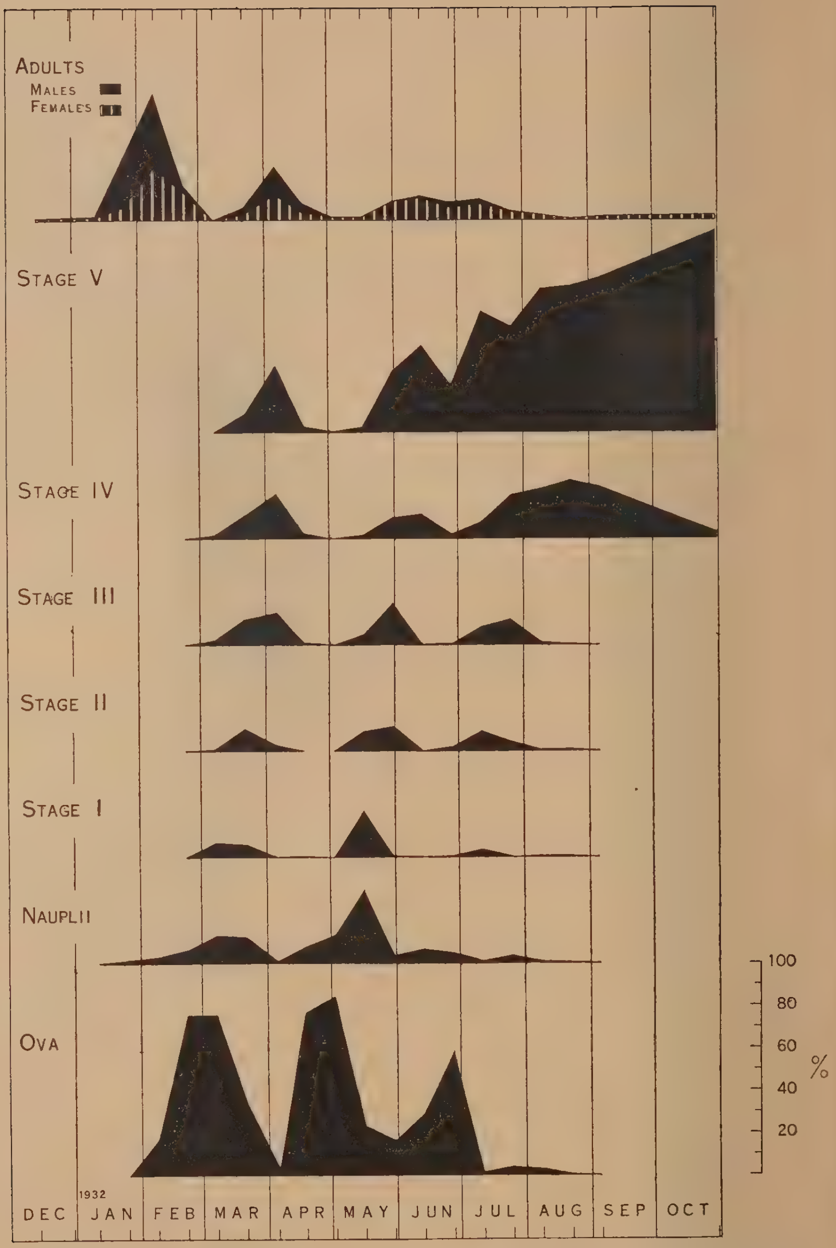
Though two peaks are thus present in the curves for the ova and nauplii during the first breeding period, only one is found a fortnight later in the Stage II copepodites, and a second reappears in the Stage V copepodites and adults. The second peak of adults (April 5th) has undoubtedly arisen from the ova of March 7th, and the ova of March 28th receive no distinct representation on these curves after Stage I copepodites ; neither do they appear to affect the curve for adults at all, these being at a minimum when the eggs of March 28th should be reaching adult stage.

From Table II it would appear that this catch of March 28th was in the nature of a " freak "—owing to the net passing through a swarm of Calanus—since, from March 7th until April 18th (neglecting March 28th), total numbers rose from 52 to 1,086 by more or less regular intervals of a few hundred each fortnight. This catch on March 28th contained 3,488 specimens and may be regarded as exceptionally and unexpectedly large.

A similar effect was produced at the end of the second breeding period (May 30th) when a minor peak occurred. It is, however, of less importance since it does not affect the curves of any of the other stages and may be regarded as a minor fluctuation in the representation of the ova.

A further question which may be raised is why ova should be present to so large an extent at Station II (Text-Figure 4) on March 21st if adults had died out by 7th and the new brood did not begin spawning until April 5th. From Table III it will be seen that the actual number of ova present on this date was only 117, and these could easily have been produced by two or three females of the autumn-winter stock which were still surviving at this time. Possibly they were producing a second brood.

It will have been seen from the Text-Figures and Plates that when catches are taken at regular intervals of a fortnight the period of reproduction can be divided into three main breeding periods, February–March, April–May, and June–July with a fourth subsidiary one early in August and that this can be applied in general to all stations. The main variations are in the number of subsidiary late summer broods at each



TEXT-FIG. 4.—Diagram illustrating the succession of breeding periods at Station II (Cock of Arran). Copepodite Stages IV and V occurring prior to March 7th, and ova and nauplii prior to February 8th have been omitted.

station (more numerous at Station I and of less importance at Station IV), and an overlapping of the first two breeding periods at Station IV owing to a lag in the starting of reproduction at this station. The cause of this has not yet been determined.

Comparison of the station inside the loch with those of the open waters showed that Calanus was still quite abundant in the early winter at Strachur when numbers outside had fallen to minimal values. This, however, was only a lag in the dying off of this population, since numbers in the loch were reduced to similar low values at a later date. Although Calanus at Station I was scarce by the middle of December it was not until late in March that it became scarce at Station IV. This lag was followed by a delay in the starting of reproduction, the first brood of eggs not appearing until the end of February, a fortnight after reproduction had begun at the stations in open waters.

Furthermore it can be stated that the enclosed waters of the loch do not form a breeding ground whence Calanus spreads to outside waters. If this had been the case evidence of such migration would have been found in the quarterly catches from Station VII and in the fortnightly catches from Station III. Those from the latter obviously followed those of Station II, and it has already been pointed out that both these stations are geographically similar.

Without more knowledge of the factors which control the development of the autumn-winter Calanus it is difficult to say why this lag occurred. That temperature is not directly concerned is fairly certain. It remains for future work to discover the actual cause.

It will have been seen that the results from this area confirm and elaborate the suggestions made by Farran (1911, p. 85) and Russell (1928, p. 444) on the course of the life cycle in Calanus.

It has been pointed out by Russell (1928, p. 434) that at certain times of the year Calanus may be found swarming at the surface during the day, even though it be a clear day with bright sunshine. This has been observed on several occasions in the Clyde Sea-Area. From March until June, and again later on, hauls at Stations I and II were divided at the 30-metre line, the object being to simplify counting by confining the diatoms to one part of the catch.

As it happened in this year diatoms were seldom rich enough to cause any difficulty of this nature. It will be noticed, however, from Tables II and III that at Station I on May 16th and at Station II on June 13th, more males, females, Stages V and IV copepodites were found in the upper 30 metres than below, a reversal of the usual condition. On both these occasions young stages and ova remained more abundant above the 30-metre line.

This will be discussed in a paper dealing with the vertical distribution of Calanus in this area.

SUMMARY.

1. Fortnightly samples were taken with a fine-meshed net in single vertical hauls at different positions in the Clyde Sea-Area.

2. Each stage of Calanus present, from ovum to adult, was counted, and charts were constructed expressing these results for one year as total numbers and as percentage composition.

3. Calanus passes the autumn and early winter mainly in its Stage V copepodite form.

4. In general, total numbers were high in September, 1931, and fell steadily to a minimum in March; in Loch Fyne the minimum occurred in April.

5. A sudden increase was observed in May and numbers rose to maximal values; the decline also was sudden.

6. Reproduction began in February and three plainly marked breeding periods were observed between February and July.

7. The time taken by the egg in developing into the adult was four weeks.

8. The total life of a Calanus during the summer was estimated to be about two and a half months; in winter it is five to six months.

9. In Loch Fyne a noticeable lag occurred during the winter and early spring.

10. The number of Calanus present in the autumn of 1932 was considerably less than at the same time in 1931. This may have been due to a shortage of food.

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TABLE I.

Date.	Station I.			Station II.			Station IV.		
	Time of Day. a.m.	Depth in Metres.	Time of Haul. m. s.	Time of Day. a.m.	Depth in Metres.	Time of Haul. m. s.	Time of Day. p.m.	Depth in Metres.	Time of Haul. m. s.
3/9/31	10.00	120	—	11.30	100	—	5.20	138	—
15/9/31	9.45	105	3 20	11.25	140	4 00	5.15	130	4 30
1/10/31	9.45	110	3 35	11.30	140	3 50	4.30	150	3 50
21/10/31	9.45	120	*4 15	11.15	135	4 15	5.00	130	4 30
5/11/31	10.35	115	3 45	noon	112	3 35	4.50	132	4 20
16/11/31	10.30	109	3 40	11.40	165	4 50			
17/11/31							8.27 (a.m.)	136	4 15
30/11/31	9.15	110	3 45	10.50	155	4 50	4.15	130	4 50
14/12/31	9.26	110	4 05	11.15	154	4 20	4.32	131	5 ca.
30/12/31	9.05	113	3 45	10.10	160	5 30	5.10	128	3 40
11/1/32	9.50	120	4 00	11.30	155	3 50	4.15	129	4 15
25/1/32	9.10	120	4 00	10.30	165	5 30	3.50	134	4 05
8/2/32	9.50	110	*3 50	11.10	170	5 45	4.45	130	4 15
22/2/32	9.05	109	3 45	10.15	153	5 30			
23/2/32							8.00 (a.m.)	—	4 40
7/3/32	9.15	110	(a)3 05 (b)1 00	10.55	154	(a)4 50 (b)1 00	4.20	128	4 10
21/3/32	10.20	115	(a)3 00 (b)1 00	11.00	161	(a)6 45 (b)1 27	4.30	126	4 45
28/3/32	9.30	110	(a)4 03 (b)1 00						
5/4/32	9.15	109	(a)3 20 (b)1 00	11.15	162	(a)5 10 (b)1 00	5.00	131	4 45
18/4/32	8.20	110	(a)3 05 (b)1 00	9.55	116	(a)3 15 (b)1 00	3.10	131	4 35
27/4/32	8.50	115	(a)3 40 (b)1 25						
2/5/32	9.29	114	(a)3 05 (b)0 56	11.00	157	(a)4 25 (b)0 55	4.42	130	4 15
16/5/32	8.15	113	(a)3 45 (b)1 05	9.50	145	(a)4 35 (b)1 05	3.05	130	5 05
23/5/32	11.00	119	(a)3 45 (b)1 03						
30/5/32	8.20	110	(a)3 00 (b)1 00	9.45	166	(a)5 35 (b)1 00	6.30	130	5 15
7/6/32	9.00	118	(a)3 40 (b)1 05						
13/6/32	8.25	115	†4 30	9.55	159	(a)4 30 (b)1 00	3.15	131	5 25
27/6/32	10.20	112	4 55	12.10 (p.m.)	158	7 40	5.25	124	4 30
11/7/32	8.20	113	4 15	10.15	152	5 35	3.50	130	4 45
25/7/32	8.20	115	(a)3 15 (b)1 02	10.10	165	(a)4 55 (b)1 00	3.05	130	4 40
8/8/32	8.20	115	(a)3 10 (b)1 00	10.15	163	(a)4 15 (b)1 00	3.30	135	4 30
22/8/32	8.25	112	3 55	9.55	158	5 45	7.15	130	4 30
5/9/32	8.50	110	4 20	10.15	165	6 50	4.05	130	4 45
30/10/32	9.15	117	3 25	11.00	144	4 50	4.15	122	3 55

APPENDIX.

	Station V.				Station VI.				Station VII.			
					p.m.				a.m.			
13/11/31	11.05 (a.m.)	92	2	50								
16/11/31					2.00	145	3	40				
17/11/31									10.25	60	1	45
22/2/32					12.20	125	3	35				
23/2/32									10.05	51	1	40
25/2/32	3.35 (p.m.)	89	3	30								
									p.m.			
30/5/32					noon	117	(a)3 (b)1	25 00	4.50	59	2	00
3/6/32	9.40 (a.m.)	90	(a)2 (b)1	25 00								
22/8/32					12.30	128	4	58	5.30	62	2	30
29/8/32	3.00 (p.m.)	88	3	20								

* Indicates that the haul was not vertical owing to state of the weather.

† Indicates that the closing apparatus failed to work and haul was not divided.

TAB

								STAT
					Nauplii.			
Date.		Ova.	I.	II.	III.	IV.	V.	VI.
3-9-31	No.	10	30	110	60	30	20	80
	%	*·7*	*2·1*	*7·6*	*4·2*	*2·1*	*1·4*	*5·5*
15-9-31	No.	1	–	–	1	2	–	–
	%	*·5*	–	–	*·5*	*1·0*	–	–
1-10-31	No.	50	2	1	3	3	–	–
	%	*44·2*	*1·8*	*·9*	*2·7*	*2·7*	–	–
21-10-31	No.	12	11	2	6	–	–	–
	%	*4·0*	*3·7*	*·7*	*2·0*	–	–	–
5-11-31	No.	–	1	–	5	6	2	3
	%	–	*1·9*	–	*9·3*	*11·1*	*3·7*	*5·6*
16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
29-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	2	–	7	–	–	–
	%	–	*3·5*	–	*12·1*	–	–	–
25-1-32	No.	1	–	–	1	–	–	–
	%	*2·5*	–	–	*2·5*	–	–	–
8-2-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
22-2-32	No.	84	4	–	2	1	–	–
	%	*56·8*	*2·7*	–	*1·4*	*·7*	–	–
7-3-32	No. (1) (2)	8 19 }27	– 3 }3	– –	– 5 }5	2 3 }5	– 2 }2	2 3 }5
	%	*51·9*	*5·8*	–	*9·6*	*9·6*	*3·8*	*9·6*
21-3-32	No. (1) (2)	70 46 }116	10 1 }11	– –	– 2 }2	– 2 }2	– 1 }1	– 4 }4
	%	*21·0*	*2·0*	–	*·4*	*·4*	*·2*	*·7*
28-3-32	No. (1) (2)	250 1150 }1400	30 130 }160	– 185 }185	10 130 }140	5 35 }40	– 25 }25	5 30 }35
	%	*40·1*	*4·6*	*5·3*	*4·0*	*1·1*	*·7*	*1·0*
5-4-32	No. (1) (2)	30 19 }49	15 2 }17	– 1 }1	– 5 }5	5 3 }8	– 2 }2	– 3 }3
	%	*6·0*	*2·1*	*·1*	*·6*	*1·0*	*·2*	*·4*
18-4-32	No. (1) (2)	60 420 }480	5 25 }30	– 35 }35	– 45 }45	– 5 }5	– 5 }5	– –
	%	*44·1*	*2·8*	*3·2*	*4·1*	*·5*	*·5*	–
27-4-32	No. (1) (2)	138 5570 }5708	90 360 }450	– 200 }200	– 20 }20	– 20 }20	– 10 }10	1 20 }21
	%	*85·3*	*6·7*	*3·0*	*·3*	*·3*	*·1*	*·3*
2-5-32	No. (1) (2)	14 7635 }7649	15 1785 }1800	– 475 }475	– 215 }215	1 100 }101	– 30 }30	– 55 }55
	%	*71·8*	*16·9*	*4·5*	*2·0*	*·9*	*·3*	*·5*
16-5-32	No. (1) (2)	64 1920 }1984	4 420 }424	10 630 }640	7 370 }377	3 200 }203	1 40 }41	2 90 }92
	%	*43·7*	*9·3*	*14·1*	*8·3*	*4·5*	*·9*	*2·0*
23-5-32	No. (1) (2)	340 360 }700	150 60 }210	90 40 }130	960 210 }1170	790 140 }930	560 110 }670	450 70 }520
	%	*4·0*	*1·2*	*·7*	*6·8*	*5·4*	*3·9*	*3·0*
30-5-32	No. (1) (2)	370 118 }488	324 13 }337	2 9 }11	4 1 }5	– –	– –	– –
	%	*20·2*	*13·9*	*·5*	*·2*	–	–	–
7-6-32	No. (1) (2)	95 370 }465	75 100 }175	– 25 }25	– 30 }30	– 20 }20	– 5 }5	– –
	%	*11·4*	*4·3*	*·6*	*·7*	*·5*	*·1*	–
13-6-32	No.	670	270	60	90	70	20	–
	%	*47·9*	*19·3*	*4·3*	*6·4*	*5·0*	*1·4*	–
27-6-32	No.	475	80	20	15	20	15	15
	%	*43·4*	*7·3*	*1·8*	*1·4*	*1·8*	*1·4*	*1·4*
11-7-32	No.	20	–	–	–	–	–	–
	%	*1·2*	–	–	–	–	–	–
25-7-32	No. (1) (2)	10 185 }195	– 15 }15	– 10 }10	5 30 }35	– –	– –	– –
	%	*15·4*	*1·2*	*·8*	*2·8*	–	–	–
8-8-32	No. (1) (2)	9 6 }15	– 1 }1	– 2 }2	– 7 }7	– 2 }2	– 2 }2	– 3 }3
	%	*3·2*	*·2*	*·4*	*1·5*	*·4*	*·4*	*·6*
22-8-32	No.	33	2	1	–	–	1	3
	%	*6·5*	*·4*	*·2*	–	–	*·2*	*·6*
5-9-32	No.	–	–	–	–		–	11
	%	–	–	–	–	–	–	*2·7*
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE II.

ION I.

Copepodites.					Adults.		
I.	II.	III.	IV.	V	♀	♂	Total.
95 *6·6*	127 *8 8*	79 *5·5*	103 *7·0*	677 *47·0*	13 *·9*	7 *·5*	1441 *99·9*
– –	1 *·5*	5 *2·5*	35 *17·2*	147 *72·1*	10 *4·9*	2 *1·0*	204 *100·2*
1 *·9*	11 *9·7*	4 *3·5*	14 *12·4*	22 *19·5*	1 *·9*	1 *·9*	113 *100·1*
– –	1 *·3*	7 *2·4*	41 *13·8*	203 *68·1*	11 *3·7*	4 *1·3*	298 *100·0*
5 *9·3*	4 *7·4*	16 *29·7*	5 *9·3*	4 *7·4*	3 *5·6*	– –	54 *100·3*
– –	– –	2 *·7*	22 *7·4*	272 *91·0*	3 *1·0*	– –	299 *100·1*
– –	– –	– –	3 *3·7*	77 *96·3*	– –	– –	80 *100·0*
– –	– –	– –	– –	4 *100·0*	– –	– –	4 *100·0*
– –	– –	– –	1 *7·1*	11 *78·6*	1 *7·1*	1 *7·1*	14 *99·9*
– –	– –	– –	2 *3·5*	37 *63·6*	2 *3·5*	8 *13·8*	58 *100·0*
– –	– –	– –	– –	18 *45·0*	7 *17·5*	13 *32·5*	40 *100·0*
– –	– –	– –	– –	4 *26·7*	4 *26·7*	7 *46·7*	15 *100·1*
– –	– –	– –	– –	– –	55 *37·2*	2 *1·4*	148 *100·2*
2 2 } 4 *7·7*	– – –	– – –	– – –	– – –	1 – } 1 *1·9*	– – –	15 37 } 52 *99·9*
– 5 } 5 *·9*	6 2 } 8 *1·5*	9 2 } 11 *2·0*	44 1 } 45 *8·2*	192 2 } 194 *35·5*	59 3 } 62 *11·4*	82 3 } 85 *15·6*	472 74 } 546 *99·8*
– 121 } 121 *3·5*	3 254 } 257 *7·4*	73 95 } 168 *4·8*	393 25 } 418 *12·0*	352 12 } 364 *10·4*	74 1 } 75 *2·2*	98 2 } 100 *2·9*	1293 2195 } 3488 *100·0*
1 14 } 15 *1·9*	1 54 } 55 *6·8*	5 123 } 128 *15·7*	60 117 } 177 *21·8*	135 56 } 191 *23·5*	75 6 } 81 *10·0*	57 24 } 81 *10·0*	384 429 } 813 *100·1*
– 3 } 3 *·3*	– – –	6 3 } 9 *·8*	120 11 } 131 *12·0*	185 21 } 206 *19·0*	95 4 } 99 *9·1*	37 2 } 39 *3·6*	508 579 } 1087 *100·0*
4 30 } 34 *·5*	2 10 } 12 *·2*	– – –	16 – } 16 *·2*	95 8 } 103 *1·5*	46 1 } 47 *·7*	16 – } 16 *·2*	408 6249 } 6657 *99·3*
– 55 } 55 *·5*	1 15 } 16 *·2*	– 1 } 1 –	6 1 } 7 *·1*	112 17 } 129 *1·2*	92 12 } 104 *1·0*	19 5 } 24 *·2*	260 10401 } 10661 *100·1*
3 146 } 149 *3·3*	– 125 } 125 *2·8*	2 125 } 127 *2·8*	11 126 } 137 *3·0*	22 68 } 90 *2·0*	36 105 } 141 *3·1*	4 7 } 11 *·2*	169 4372 } 4541 *100·0*
2490 1040 } 3530 *20·4*	3360 1060 } 4420 *25·5*	1840 520 } 2360 *13·6*	770 143 } 913 *5·3*	890 86 } 976 *5·6*	730 27 } 757 *4·4*	40 – } 40 *·2*	13460 3866 } 17326 *100·0*
2 5 } 7 *·3*	32 94 } 126 *5·2*	332 200 } 532 *22·0*	634 118 } 752 *31·1*	58 30 } 88 *3·6*	42 22 } 64 *2·6*	8 – } 8 *·3*	1808 610 } 2418 *99·9*
– 5 } 5 *·1*	5 5 } 10 *·2*	40 15 } 55 *1·3*	1035 89 } 1124 *26·9*	1515 37 } 1552 *38·0*	560 3 } 563 *13·8*	65 – } 65 *1·6*	3390 704 } 4094 *99·5*
20 *1·4*	– –	– –	53 *3·8*	125 *8·9*	15 *1·1*	5 *·4*	1398 *99·9*
8 *·7*	39 *3·6*	43 *3·9*	28 *2·6*	120 *11·0*	205 *18·7*	12 *1·1*	1095 *100·1*
32 *1·9*	183 *10·8*	264 *15·6*	219 *13·0*	852 *50·4*	92 *5·4*	28 *1·7*	1690 *100·0*
10 – } 10 *·8*	15 – } 15 *1·2*	37 1 } 38 *3·0*	430 11 } 441 *34·8*	342 9 } 351 *27·7*	129 5 } 134 *10·6*	24 – } 24 *1·9*	1002 266 } 1268 *100·2*
1 6 } 7 *1·5*	76 23 } 99 *21·2*	171 9 } 180 *38·4*	59 5 } 64 *13·7*	63 4 } 67 *14·3*	13 2 } 15 *3·2*	4 – } 4 *·9*	396 72 } 468 *99·9*
6 *1·2*	2 *·4*	15 *3·0*	135 *26·8*	287 *56·9*	10 *2·0*	9 *1·8*	504 *100·0*
26 *6·3*	38 *9·2*	27 *6·6*	42 *10·2*	228 *55·5*	29 *7·0*	10 *2·4*	411 *99·9*
– –	– –	– –	11 *3·1*	329 *93·5*	12 *3·4*	– –	352 *100·0*

TAB

STAT

					Nauplii.			
Date.		Ova.	I.	II.	III.	IV.	V.	VI.
3-9-31	No.	970	–	–	380	–	–	–
	%	*45·5*	–	–	*17·8*	–	–	–
15-9-31	No.	–	–	–	79	2	–	1
	%	–	–	–	*2·1*	*·1*	–	–
1-10-31	No.	25	–	–	25	–	–	–
	%	*·5*	–	–	*·5*	–	–	–
21-10-31	No.	3	–	3	3	–	–	–
	%	*·1*	–	*·1*	*·1*	–	–	–
5-11-31	No.	–	–	–	–	–	–	–
		–	–	–	–	–	–	–
16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-1-32	No.	–	1	–	2	–	–	–
	%	–	*·5*	–	*1·0*	–	–	–
8-2-32	No.	41	6	–	1	–	–	–
	%	*17·6*	*2·6*	–	*·4*	–	–	–
22-2-32	No.	231	8	–	8	1	1	2
	%	*76·0*	*2·6*	–	*2·6*	*·4*	*·4*	*·7*
7-3-32	No. (1)	– } 119	– } 4	– } 4	– } 4	– } 5	– } 1	– } 3
	(2)	119	4	4	4	5	1	3
	%	*75·8*	*2·6*	*2·6*	*2·6*	*3·2*	*·6*	*1·9*
21-3-32	No. (1)	– } 117	– } 10	– } 9	– } 11	– } 4	– } 4	– } 5
	(2)	117	10	9	11	4	4	5
	%	*34·0*	*2·9*	*2·6*	*3·2*	*1·2*	*1·2*	*1·5*
5-4-32	No. (1)	4 } 17	– } 3	– } 1	–	– } 1	–	–
	(2)	13	3	1		1		
	%	*3·4*	*·6*	*·2*	–	*·2*	–	–
18-4-32	No. (1)	33 } 346	3 } 18	– } 12	– } 3	– } 2	– } 1	–
	(2)	313	15	12	3	2	1	–
	%	*77·2*	*4·0*	*2·7*	*·7*	*·5*	*·2*	–
2-5-32	No. (1)	22 } 34622	13 } 3933	1 } 1241	– } 190	– } 70	– } 50	– } 50
	(2)	34600	3920	1240	190	70	50	50
	%	*84·3*	*9·6*	*3·0*	*·5*	*·2*	*·1*	*·1*
16-5-32	No. (1)	506 } 876	148 } 238	76 } 326	92 } 272	44 } 134	20 } 150	28 } 168
	(2)	370	90	250	180	90	130	140
	%	*23·6*	*6·4*	*8·8*	*7·3*	*3·6*	*4·0*	*4·5*
30-5-32	No. (1)	370 } 547	57 } 90	– } 30	– } 13	–	–	–
	(2)	177	33	30	13			
	%	*16·9*	*2·8*	*·9*	*·4*	–	–	–
13-6-32	No. (1)	178 } 498	66 } 88	2 } 12	– } 6	– } 1	– } 1	–
	(2)	320	22	10	6	1	1	–
	%	*29·5*	*5·2*	*·7*	*·4*	*·1*	*·1*	–
27-6-32	No.	582	32	6	4	–	–	8
	%	*58·4*	*3·2*	*·6*	*·4*	–	–	*·8*
11-7-32	No.	31	1	1	7	6	6	6
	%	*1·6*	–	–	*·4*	*·3*	*·3*	*·3*
25-7-32	No. (1)	13 } 53	3 } 19	– } 12	1 } 17	–	–	–
	(2)	40	16	12	16			
	%	*4·1*	*1·5*	*·9*	*1·3*	–	–	–
8-8-32	No. (1)	19 } 46	2 } 8	– } 3	– } 8	– } 1	–	– } 2
	(2)	27	6	3	8	1		2
	%	*2·9*	*·5*	*·2*	*·5*	–	–	*·1*
22-8-32	No.	14	2	2	2	–	–	–
	%	*·6*	*·1*	*·1*	*·1*	–	–	–
5-9-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE III

ION II

Copepodites.					Adults.		
I.	II.	III.	IV.	V.	♀	♂	Total.
–	3	32	387	334	19	10	2135
–	*·1*	*1·6*	*18·1*	*15·6*	*·9*	*·5*	*100·1*
–	19	179	660	2876	19	8	3843
–	*·5*	*4·7*	*17·2*	*74·9*	*·5*	*·2*	*100·2*
–	–	20	395	4320	20	5	4810
–	–	*·4*	*8·2*	*89·9*	*·4*	*·1*	*100·1*
–	–	–	135	2398	10	–	2552
–	–	–	*5·3*	*94·0*	*·4*	–	*100·0*
–	–	1	15	134	5	–	155
–	–	*·7*	*9·7*	*86·5*	*3·2*	–	*100·1*
–	–	–	190	5975	10	–	6175
–	–	–	*3·1*	*96·8*	*·2*	–	*100·1*
–	–	–	64	2038	4	2	2108
–	–	–	*3·0*	*96·7*	*·2*	*·1*	*100·0*
–	–	–	3	176	2	–	181
–	–	–	*1·7*	*97·2*	*1·1*	–	*100·0*
–	–	–	18	968	6	9	1001
–	–	–	*1·8*	*96·8*	*·6*	*·9*	*100·1*
–	–	–	3	506	8	25	542
–	–	–	*·5*	*93·5*	*1·5*	*4·6*	*100·1*
–	–	–	2	137	13	51	206
–	–	–	*1·0*	*66·5*	*6·3*	*24·8*	*100·1*
–	–	–	–	45	58	82	233
–	–	–	–	*19·3*	*24·9*	*35·2*	*100·0*
–	–	–	–	2	39	12	304
–	–	–	–	*·7*	*12·8*	*3·9*	*100·1*
– 11 } 11	– 1 } 1	3 – } 3	2 – } 2	– –	– –	– –	5 152 } 157
7·0	*·6*	*1·9*	*1·3*	–	–	–	*100·1*
– 20 } 20	– 36 } 36	6 35 } 41	24 13 } 37	27 2 } 29	9 – } 9	12 – } 12	78 266 } 344
5·8	*10·5*	*11·9*	*10·8*	*8·4*	*2·6*	*3·5*	*100·1*
–	– 14 } 14	1 75 } 76	19 87 } 106	102 55 } 157	55 6 } 61	59 7 } 66	240 262 } 502
–	*2·8*	*15·1*	*21·1*	*31·3*	*12·1*	*13·1*	*99·9*
– 2 } 2	–	– 4 } 4	3 8 } 11	4 10 } 14	11 4 } 15	11 9 } 20	65 383 } 448
·5	–	*·9*	*2·5*	*3·1*	*3·3*	*4·5*	*100·1*
– 17 } 17	– 17 } 17	– 15 } 15	3 1 } 4	219 7 } 226	520 32 } 552	98 20 } 118	876 40229 } 41105
–	–	–	–	*·6*	*1·3*	*·3*	*100·0*
54 750 } 804	90 240 } 330	52 119 } 171	30 33 } 63	96 3 } 99	41 8 } 49	23 6 } 29	1400 2309 } 3709
21·7	*8·9*	*4·6*	*1·7*	*2·7*	*1·3*	*·8*	*99·9*
– 10 } 10	– 380 } 380	10 617 } 627	97 223 } 320	897 33 } 930	280 3 } 283	3 – } 3	1714 1519 } 3233
·3	*11·7*	*19·4*	*9·9*	*28·8*	*8·8*	*·1*	*100·0*
– 1 } 1	–	– 3 } 3	19 176 } 195	251 446 } 697	17 153 } 170	1 18 } 19	534 1157 } 1691
·1	–	*·2*	*11·5*	*41·2*	*10·6*	*1·1*	*100·7*
7	18	6	20	226	59	28	996
·7	*1·8*	*·6*	*2·0*	*22·7*	*5·9*	*2·8*	*99·9*
74	186	174	163	1138	149	51	1993
3·7	*9·3*	*8·7*	*8·2*	*57·1*	*7·5*	*2·6*	*100·0*
– 3 } 3	– 59 } 59	14 141 } 155	161 107 } 268	617 36 } 653	51 – } 51	7 4 } 11	867 434 } 1301
·2	*4·5*	*11·9*	*20·6*	*50·2*	*3·9*	*·8*	*99·9*
– 6 } 6	– 5 } 5	6 15 } 21	351 21 } 372	1039 33 } 1072	35 3 } 38	11 – } 11	1463 130 } 1593
·4	*·3*	*1·3*	*23·4*	*67·3*	*2·4*	*·7*	*100·0*
14	18	6	650	1638	26	6	2378
·6	*·8*	*·3*	*27·3*	*68·9*	*1·1*	*·3*	*100·2*
–	–	5	675	2015	50	15	2760
–	–	*·2*	*24·5*	*73·0*	*1·8*	*·5*	*100·0*
–	–	–	22	755	18	–	795
–	–		*2·8*	*94·9*	*2·3*	–	*100·0*

TAB

STAT

Date.		Ova.			Nauplii.			
			I.	II.	III.	IV.	V.	VI
3-9-31	No.	40	30	20	150	170	100	80
	%	*·4*	*·3*	*·2*	*1·4*	*1·5*	*·9*	*·7*
15-9-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
1-10-31	No.	100	–	–	50	10	–	–
	%	*·8*	–	–	*·4*	*·1*	–	–
21-10-31	No.	14	21	–	7	–	–	–
	%	*·2*	*·3*	–	*·1*	–	–	–
5-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
17-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
29-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
8-2-32	No.	20	–	–	–	–	–	–
	%	*·7*	–	–	–	–	–	–
23-2-32	No.	9	–	–	–	–	–	–
	%	*·7*	–	–	–	–	–	–
7-3-32	No.	156	19	4	3	2	–	–
	%	*37·0*	*4·5*	*1·0*	*·7*	*·5*	–	–
21-3-32	No.	226	54	66	16	1	–	–
	%	*58·7*	*14·0*	*17·1*	*4·2*	*·3*	–	–
5-4-32	No.	103	5	27	20	3	2	2
	%	*53·4*	*2·6*	*14·0*	*10·4*	*1·6*	*1·0*	*1·0*
18-4-32	No.	59	22	9	4	2	1	1
	%	*38·1*	*14·2*	*5·8*	*2·6*	*1·3*	*·6*	*·6*
2-5-32	No.	406	25	8	3	2	4	8
	%	*74·9*	*4·6*	*1·5*	*·6*	*·4*	*·7*	*1·5*
16-5-32	No.	150	50	70	80	100	60	50
	%	*7·1*	*2·4*	*3·3*	*3·8*	*4·8*	*2·9*	*2·4*
30-5-32	No.	455	295	65	20	25	15	15
	%	*37·5*	*24·4*	*5·4*	*1·7*	*2·1*	*1·2*	*1·2*
13-6-32	No.	990	115	40	25	20	15	30
	%	*47·6*	*5·5*	*1·9*	*1·2*	*·9*	*·7*	*1·4*
27-6-32	No.	1800	350	165	90	30	40	55
	%	*58·2*	*11·3*	*5·3*	*2·9*	*1·0*	*1·3*	*1·8*
11-7-32	No.	49	9	6	4	3	2	1
	%	*2·2*	*·4*	*·3*	*·2*	*·1*	*·1*	–
25-7-32	No.	3	–	–	–	–	–	–
	%	*·1*	–	–	–	–	–	–
8-8-32	No.	15	8	3	–	–	–	–
	%	*·7*	*·4*	*·1*	–	–	–	–
22-8-32	No.	3	–	–	–	–	–	–
	%	*·3*	–	–	–	–	–	–
5-9-32	No.	9	3	2	1	–	–	–
	%	*1·0*	*·3*	*·2*	*·1*	–	–	
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

TAB

STAT

Date.		Ova.			Nauplii.			
			I.	II.	III.	IV.	V.	VI.
13-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-2-32	No.	2	1	–	3	–	–	1
	%	*25·0*	*12·5*	–	*37·5*	–	–	*12·5*
3-6-32	No.	921	303	120	4	–	–	2
	%	*60·7*	*20·0*	*7·9*	*·3*	–	–	*·1*
29-8-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

STAT

16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
22-2-32	No.	155	24	–	34	29	20	56
	%	*43·6*	*6·8*	–	*9·6*	*8·2*	*5·6*	*15·8*
30-5-32	No.	288	74	15	–	–	–	–
	%	*13·4*	*3·4*	*·7*	–	–	–	–
22-8-32	No.	–	1	1	2	–	2	5
	%	–	*·2*	*·2*	*·3*	–	*·3*	*·9*

STAT

17-11-31	No.	–	–	–	1		–	–
	%	–	–	–	*10·0*	–	–	–
23-2-32	No.	2	–	–	–	–	1	1
	%	*20·0*	–	–	–	–	*10·0*	*10·0*
30-5-32	No	5	5	–	15	15	20	25
	%	*·1*	*·1*	–	*·4*	*·4*	*·6*	*·7*
22-8-32	No	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE IV.

ION IV.

		Copepodites.			Adults.		
I.	II.	III.	IV.	V.	♀	♂	Total.
120	140	170	90	9960	–	–	11070
1·1	*1·3*	*1·5*	*·8*	*90·0*	–	–	*100·1*
20	10	30	90	8310	30	–	8490
·2	*·1*	*·4*	*1·1*	*97·9*	*·4*	–	*100·1*
–	–	–	10	11970	50	10	12200
–	–	–	*·1*	*98·1*	*·4*	*·1*	*100·0*
–	7	–	7	7650	7	–	7713
–	*·1*	–	*·1*	*99·2*	*·1*	–	*100·1*
–	–	–	10	8290	10	–	8310
–	–	–	*·1*	*99·8*	*·1*	–	*100·0*
–	–	–	30	7420	–	–	7450
–	–	–	*·4*	*99·6*	–	–	*100·0*
–	–	–	15	5120	5	–	5140
–	–	–	*·3*	*99·6*	*·1*	–	*100·0*
–	–	–	30	3750	–	–	3780
–	–	–	*·8*	*99·2*	–	–	*100·0*
–	–	–	7	3087	10	10	3114
–	–	–	*·2*	*99·1*	*·3*	*·3*	*99·9*
–	–	–	2	2070	4	10	2086
–	–	–	*·1*	*99·3*	*·2*	*·5*	*100·1*
–	–	–	8	2685	37	128	2858
–	–	–	*·3*	*93·9*	*1·3*	*4·5*	*100·0*
–	–	–	10	2515	58	348	2951
–	–	–	*·3*	*85·3*	*1·9*	*11·8*	*100·0*
–	–	–	2	1056	28	113	1208
–	–	–	*·2*	*87·4*	*2·3*	*9·4*	*100·0*
1	–	–	–	142	46	48	421
·2	–	–	–	*33·8*	*10·9*	*11·4*	*100·0*
–	–	–	1	7	8	6	385
·	–	–	*·3*	*1·8*	*2·1*	*1·6*	*100·1*
10	1	–	1	8	8	3	193
5·2	*·5*	–	*·5*	*4·1*	*4·1*	*1·6*	*100·0*
–	3	2	10	22	17	3	155
–	*1·9*	*1·3*	*6·5*	*14·2*	*11·0*	*1·9*	*100·0*
6	1	5	38	21	13	2	542
1·1	*·2*	*·9*	*7·0*	*3·9*	*2·4*	*·4*	*100·1*
56	187	796	314	122	38	28	2101
2·7	*8·9*	*37·9*	*14·9*	*5·8*	*1·8*	*1·3*	*100·0*
22	53	44	39	132	16	13	1209
1·8	*4·4*	*3·6*	*3·2*	*10·9*	*1·3*	*1·1*	*99·8*
70	40	30	80	501	102	17	2075
3·4	*1·9*	*1·4*	*3·8*	*24·1*	*4·9*	*·8*	*99·5*
60	93	93	36	177	102	3	3094
1·9	*3·0*	*3·0*	*1·2*	*5·7*	*3·3*	*·1*	*100·0*
13	21	104	326	1537	127	13	2218
·6	*·9*	*4·7*	*14·7*	*69·4*	*5·7*	*·6*	*99·9*
–	3	27	682	1520	111	4	2350
–	*·1*	*1·1*	*29·0*	*64·7*	*4·7*	*·2*	*99·9*
–	1	–	610	1442	36	3	2115
–	–	–	*28·8*	*68·1*	*1·7*	*·1*	*99·9*
–	–	2	311	743	16	2	1077
–	–	*·2*	*28·9*	*69·0*	*1·5*	*·2*	*100·1*
–	4	2	290	609	19	2	941
–	*·5*	*·2*	*30·8*	*64·7*	*2·0*	*·2*	*100·0*
–	–	–	96	1110	5	1	1212
–	–	–	*7·9*	*91·6*	*·4*	*·1*	*100·0*

LE V.

ION V.

		Copepodites.			Adults		
I.	II.	III.	IV.	V.	♀	♂	Total.
–	–	2	4	22	1	·	29
–	–	*6·9*	*13·8*	*75·9*	*3·5*	·	*100·1*
–	–	–	–	–	1	–	8
–	–	–	–	–	*12·5*	–	*100·0*
2	16	59	53	15	18	1	1514
·1	*1·1*	*3·9*	*3·5*	*1·0*	*1·2*	*·1*	*99·9*
–	–	12	64	90	11	2	179
–	–	*6·7*	*35·8*	*50·3*	*6·1*	*1·1*	*100·0*

ION VI.

–	–	1	20	625	2	–	648
–	–	*·1*	*3·1*	*96·5*	*·3*	–	*100·0*
12	–	–	–	3	8	14	355
3·4	–	–	–	*·8*	*2·3*	*3·9*	*100·0*
5	81	412	607	418	247	8	2155
·2	*3·8*	*19·1*	*28·2*	*19·4*	*11·5*	*·4*	*100·1*
10	31	27	89	389	16	6	579
1·7	*5·4*	*4·7*	*15·4*	*67·2*	*2·3*	*1·0*	*100·1*

ION VII

1	–		–	8	–	–	10
10·0	–	–	–	*80·0*	–	–	*100·0*
–	–	–	–	5	–	1	10
–	–	–	–	*50·0*	–	*10·0*	*100·0*
165	485	1610	930	74	2	1	3352
4·9	*14·5*	*48·0*	*27·8*	*2·2*	*·1*	–	*99·8*
–	6	10	12	72		2	103
–	*5·8*	*9·7*	*11·7*	*69·9*	*1·0*	*1·9*	*100·0*

On the Biology of *Calanus finmarchicus.* II. Seasonal Variations in the Size of *Calanus finmarchicus* in the Clyde Sea-Area.

By

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Naturalist at the Marine Station, Millport.

With Eight Figures in the Text.

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INTRODUCTION.

THE size of copepods varies considerably both from place to place and also during the course of the year. Several hypotheses have been put forward to explain this fact.

The variations in size of the same species from different localities or depths are sometimes correlated with slight morphological differences, and this has led Steuer (1925, 1931, 1932) to suppose that the differences indicate geographical or habitat races and that the species may be in process of splitting up into several. The larger varieties are commonly found in the colder part of the range and the smaller in the warmer part, but this does not invariably hold. On the other hand, a single catch of copepods sometimes shows animals of such a great range of size that some observers (Sewell, 1912 ; Gurney, 1929) think that they cannot have been produced from the previous developmental stage by one moult only and have supposed that an extra moult must take place to account for the larger specimens or a moult be missed to account for the smaller.

It was therefore thought of interest to measure samples of *Calanus finmarchicus* from several stations in the Clyde Sea-Area over the course of a year to find out what amount of size variation occurred.

The Calanus used for the purpose were those taken by Dr. A. G. Nicholls in his fortnightly hauls from three different stations in the Clyde

Sea-Area and the preceding paper must be referred to for the details about the stations worked and hauls taken. The Calanus had already been picked out from the catches and the developmental stages separated and I am much indebted to him for the use of this prepared material.

Only adults (male and female), Stage V, and Stage IV Calanus were measured since it was thought that this would be enough to show variations clearly. The length measured was that of the cephalothorax and in the curves of Figures 2, 4, and 6 it is the median length which is graphed. None of the stages chosen was present in sufficiently large numbers for measurement during the whole year and it is unfortunate that at two of the stations adults were lacking during one of the most interesting times of the year. The number aimed at for measurement was in most cases about a hundred and when the catch was a large one it was sub-sampled. The adults often fell short of this number however, and, during the summer, vertical hauls with a one metre stramin net were also made at each station and the adults picked out and measured. Such hauls were not used for Stage V because it was thought that a few of the smaller specimens might escape through the meshes of the net and so give a false impression of the size. Towards the end of the summer when female Calanus were small in size a few of these too may have been lost in this way, but the number would be too small to affect the results appreciably.

In general, the sizes of the Calanus measured were greatest in spring (March–April) and smallest towards the end of the summer and the beginning of autumn, which is in accordance with results obtained elsewhere (Adler and Jespersen, 1920). There are, however, numerous variations in size throughout the summer both between different stages at the same station, and between different stations. The maximum size is not found for all stages on the same date nor on the same date at all stations. It will therefore be advisable to take each station separately.

Station I (Figs. 1 and 2).

Only Stage V Calanus were present to any extent during the autumn, and even these were not always present in numbers sufficient for measurement. The size appears to fluctuate considerably, being least in September and rising in December and January. This autumn brood of Calanus began to moult into adults in January, after which Stage V disappeared until the middle of March when the offspring of these adults had developed. After that, most stages were usually present.

The adult females found on February 22nd were those which had survived the autumn as Stage V, and were of medium size. The next occasion on which there were enough to measure was March 21st (Nicholls' first brood, see p. 88) and there was a great increase in size. These

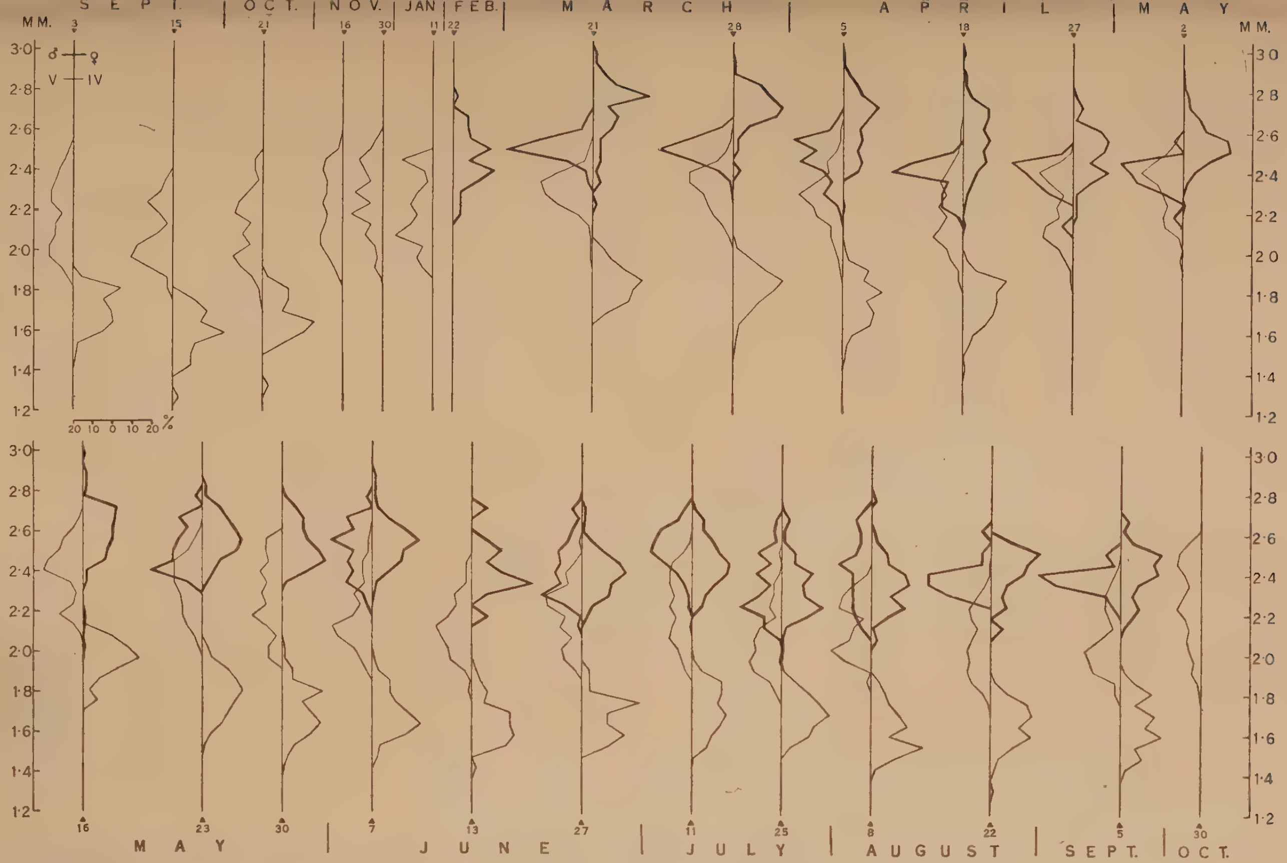

FIG. 1.—The percentage size distribution of Calanus at Station I from September, 1931, to October, 1932. Left-hand side : thick line males, thin line Stage V ; right-hand side : thick line females, thin line Stage IV.

females were the biggest found during the whole year (median length 2·76 mm.); there was a wide range of sizes, but the mode was well towards the upper limit (Fig. 1). This was four weeks after the appearance of a large egg maximum, the product of the medium sized females, and these large specimens were therefore the offspring of the autumn-winter brood which had survived from 1931. Succeeding weeks showed gradually decreasing sizes until on April 27th they were not much larger than the autumn-winter brood. These smaller females laid a great quantity of eggs (April 18th–May 2nd) which appeared as adults in the catches from May 16th–June 7th and were again larger, although not so large as those of the first brood. On June 13th there was a very sudden and marked drop in size (median length 2·40 mm.) and at the same time a great number of eggs was laid. A month later these eggs had produced females slightly larger than those of June 13th, but the size had so much decreased that they were slightly smaller than the autumn-winter brood. On July 25th there was another drop in size to the minimum found during the whole year, and at the same time there was a large proportion of eggs in the catch. A month later, on August 22nd, these developed into larger females, almost the same size as the autumn-winter brood. The size curves (Fig. 1) for this date and for July 11th are more compact and have a better defined mode than those for intermediate weeks, indicating a more homogeneous population. The size remained very much the same on September 5th, but after this females became very scarce and were no longer present in quantities sufficient to measure.

It is obvious that the largest females developed during the end of February and the beginning of March when the sea-water was at its coldest, and that the smallest females, those of July 27th, developed in water which was at its maximum temperature for the year. But between these extremes there was a series of increases and decreases in size which cannot be explained on the basis of temperature alone, but which were connected rather with the breeding periods. The largest proportion of eggs in the catches was found when the females were at a size minimum and usually when they were few in number (cf. the preceding paper, p. 95). Exactly a month later than this females of a maximal size were found. Thus, for example, there was an egg maximum on February 22nd and the females on March 21st were large; this held for the periods June 13th–July 11th, July 25th–August 22nd, and probably also for the April to May period, but this was a larger and more spread out egg maximum and the females produced from these eggs were not so clearly marked off. The period from the maximum of size to the production of eggs varied, being a month in the first case (March 21st–April 18th), but much less later on in the year, e.g. July 11th–25th.

The curve of median sizes for males does not follow quite the same course. Males were scarce after the end of March and could not be measured for every station worked. Their first appearance in numbers sufficient for measurement was on March 21st when they were of large size and must have belonged to the large first brood. After this they, like the females, decreased in size till the end of April. Their increase to a secondary maximum again was delayed until May 23rd and 30th, but there followed a sharp drop in size which is not apparent till June 27th since there were not enough to measure on June 13th. The actual minimum would in all probability have been found on June 13th since it occurred on that date for all other stages. The rise to maximal size again on July 11th was well marked and on this date the males were the largest found during the year (median length 2·53 mm.). There was again, as with females, a drop in size to July 25th and a subsequent rise.

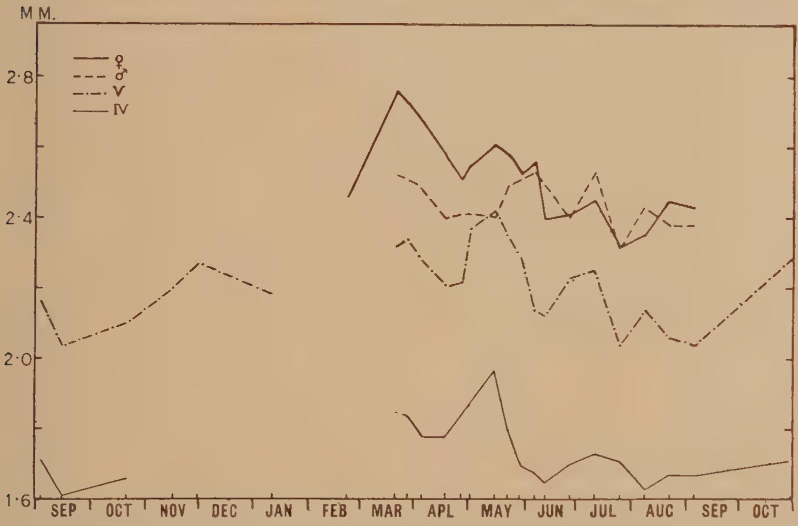

Fig. 2.—The median length of the Calanus measured at Station I (male, female, Stage V and Stage IV) during 1931 and 1932.

The curve for Stage V Calanus corresponded much more closely with the curve for females than did that for males. There were the four well defined maxima on March 21st–28th, May 16th, July 11th, and August 8th and the intermediate minima on April 18th–27th, June 13th, and July 25th. The maximum size for the year was found on May 16th (median length 2·42 mm.) and the minimum on July 25th (median length 2·04 mm.) and in the beginning of September (both in 1931 and 1932). After September, 1932, there was another increase in size and, as mentioned already, sizes fluctuated a good deal during the autumn.

Since the time usually spent as Stage V is probably only four or five days and Stations were taken only once a fortnight, it is not surprising that Stage V and adults should agree closely. Stage IV, being eight to ten days behind in development, might be expected to show peaks sometimes on the same date as adults, sometimes a week or a fortnight before. Accordingly there is only a rough agreement between the respective curves. There was a well defined maximum (when Stage IV reached its largest size of 1·97 mm. for the year) on May 16th and a subsequent marked fall to a minimum on June 13th. The smallest sizes were found on this date and in September, 1931, and August, 1932 (median length 1·62–1·65 mm.).

The size curves (Fig. 1) as a whole show a great range and no well marked mode. This is especially so with females and Stage V. On March 21st, however, the curves for all stages were more compact and had a definite mode. This is probably because the first brood appearing then develops from eggs laid within a comparatively short space of time and forms a more homogeneous population than during the rest of the year. The appearance of a new brood of maximal size had the same effect on a few other occasions (e.g. males and females on July 11th ; Stage IV on May 16th). Later in the year several hundred Stage V and Stage IV were measured to see if inadequate numbers were the cause of the irregular curves, but this was not the case.

STATION II (Figs. 3 and 4).

Station II was worked only once a fortnight and, in addition, adult Calanus were too few to measure on several occasions during the March to May period, so that the size curves do not give the same picture as those of Station I. The autumn-winter brood of adults appeared, the males in January and the beginning of February and the females in February. After this they became scarce and on March 21st, the date when at Station I the largest females were found, there were not enough to measure, so that the period of maximum size, on the first appearance of the first brood, has probably been missed. On April 5th the first brood was larger than the autumn-winter brood, but not markedly so. In the females there was a subsequent decrease to May 2nd when there was a great production of eggs. At Station I the females appearing a month later than the eggs were much larger, but this was not so at Station II ; the size remained constant or rose only slightly and the striking feature is the sudden drop in size which occurred on June 13th (as at Station I) and on August 8th (a fortnight later than at Station I). In the end of August and September the females found were the smallest for the year.

The curve for male sizes does not much resemble that for females. The largest males found were those of the autumn-winter brood found on January 11th ; the first-brood males may have been larger on their first

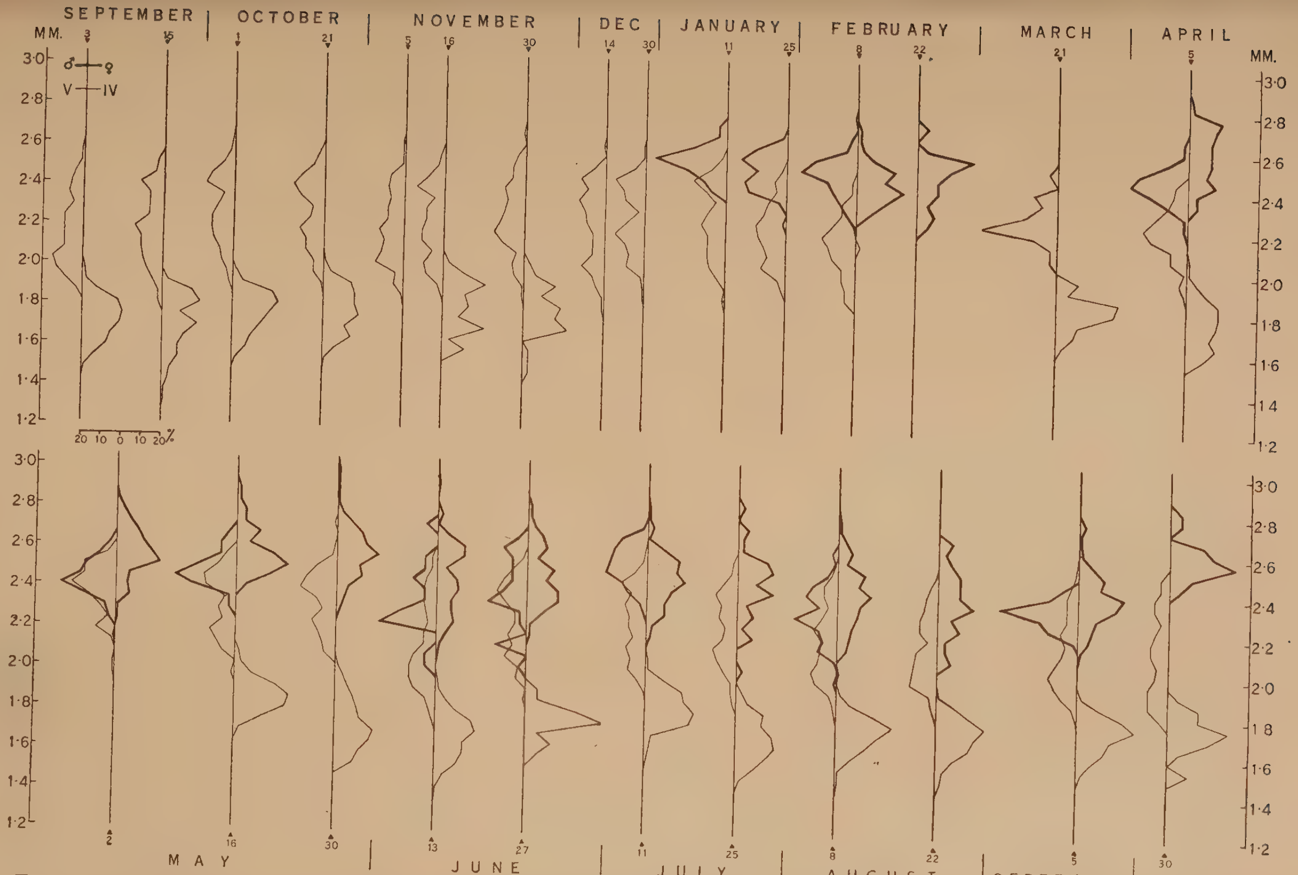

FIG. 3.—The percentage size distribution of Calanus at Station II from September, 1931, to October, 1932. Left-hand side: thick line males, thin line Stage V; right-hand side: thick line females, thin line Stage IV.

appearance, but on April 5th they were slightly smaller and decreased in size further till April 30th. There was a slight rise on May 16th, the usual fall on June 13th, when the smallest males for the year were found, and a subsequent rise to a maximum on July 11th (found also at Station I) when they were nearly as large as the autumn-winter brood. Like the females they decreased in size again at the end of August.

The Stage V curve shows as little agreement with the female as does the male. The size during the autumn varied considerably, and those of the first brood measured on March 21st were no larger than the majority of the autumn-winter stock. The size curve (Fig. 3) for that date, however, is very different; instead of having a wide range of sizes and no definite mode, it is shorter and has a well marked mode. There is no definite increase in size till May 2nd (not a date which corresponds with any of the other stages), but there was the usual marked fall on June 13th to a size smaller than that found during the rest of the year. June 27th showed a marked rise and there was a gradual fall thereafter until September.

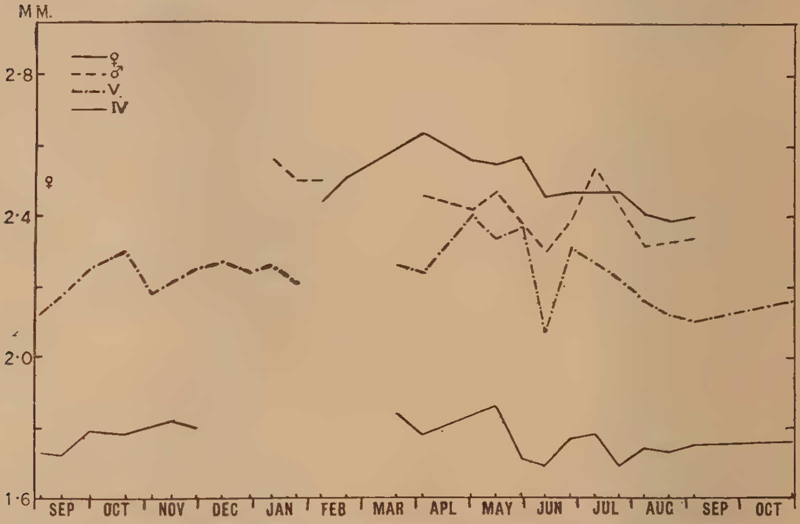

Fig. 4.—The median length of the Calanus measured at Station II (male, female, Stage V, and Stage IV) during 1931 and 1932.

The curve for Stage IV shows only a rough agreement. There was a maximum on May 16th (with a well marked mode on the size curve), a fall to June 13th, a rise and then a further fall on July 25th.

Station IV (Figs. 5 and 6).

Station IV differed in several respects from the other two stations. During the autumn the Stage V Calanus were considerably larger than

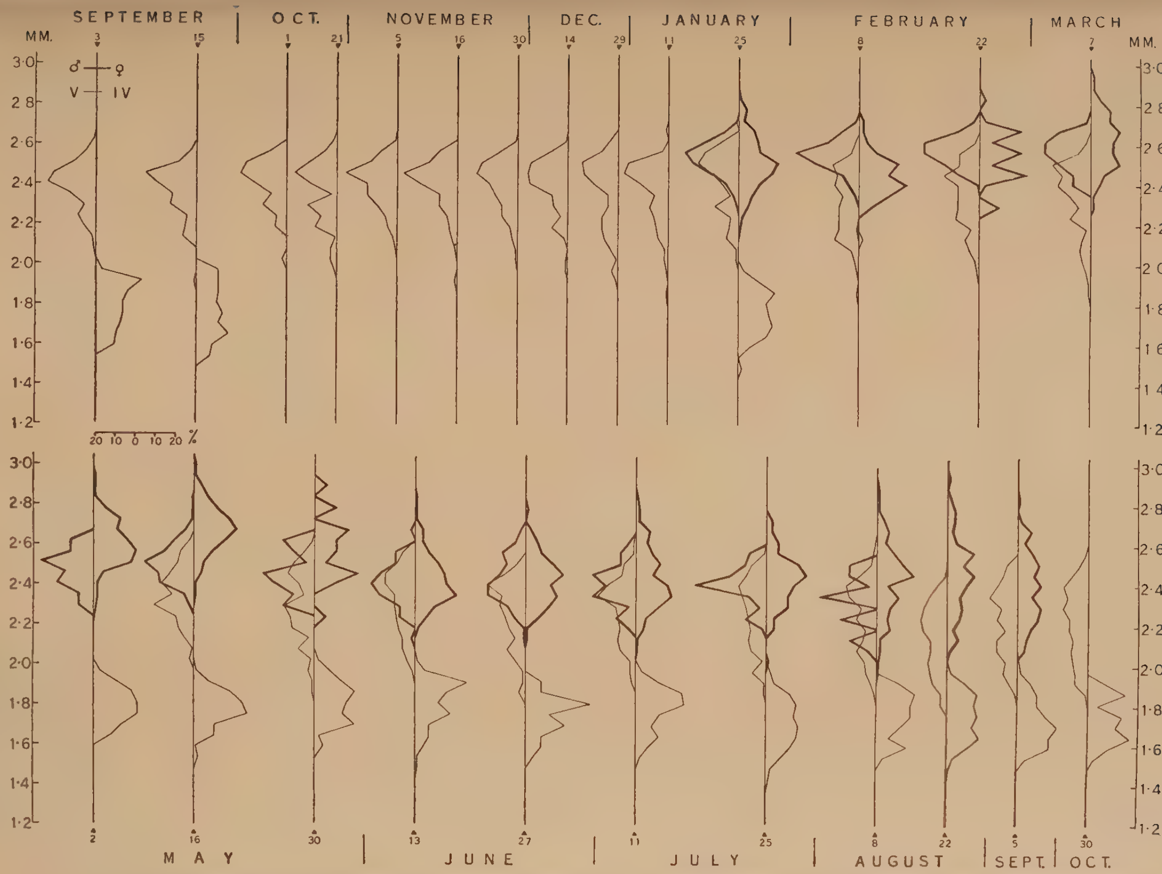

FIG. 5.—The percentage size distribution of Calanus at Station IV from September, 1931, to October, 1932. Left-hand side: thick line males, thin line Stage V; right-hand side: thick line females, thin line Stage IV.

those from elsewhere, and the size curves (Fig. 5), although showing, like the other stations, a wide range of sizes, usually had a well defined mode near the upper limit. The size also remained much more constant throughout the autumn, owing probably to geographical conditions. The deep water of upper Loch Fyne is separated from the rest of the area by two shallow bars enclosing a basin not more than 65 metres in depth, where there is, according to Mill (1889–91), much less movement of the water by tides and winds than outside. The Calanus must therefore form a more constant and homogeneous population than at the other stations.

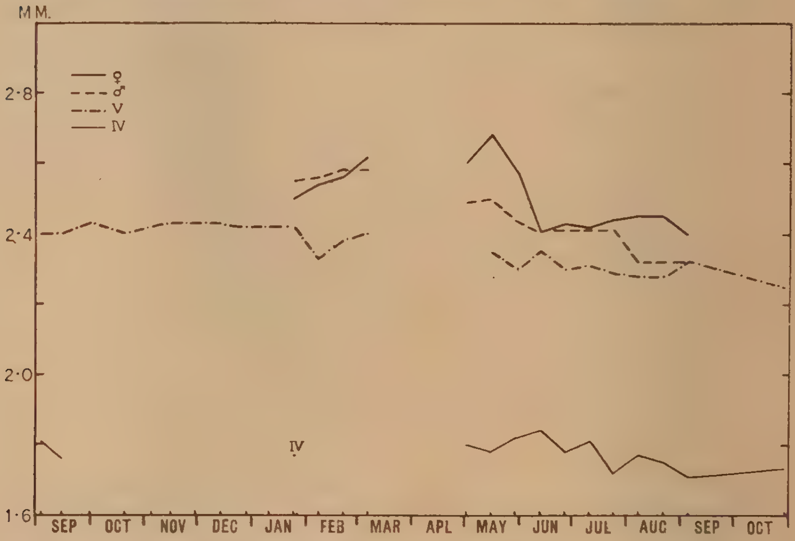

Fig. 6.—The median length of the Calanus measured at Station IV (male, female, Stage V, and Stage IV) during 1931 and 1932.

Adults first appeared on January 25th, males being then more numerous than females, and at the same time there was a distinct drop in the size of Stage V Calanus (Fig. 6) which indicates that the larger specimens moulted first. However, there was a subsequent recovery in the size of Stage V and at the same time the size of both male and female increased slightly. At first the male was a little the larger, but by March 7th the female had surpassed it. After this Calanus became too scarce to measure until May 2nd, so that measurements for the first brood have here been missed completely. The females present on May 2nd were much the same size as those of March 7th, and there was a large proportion of eggs in the catch, as indeed there had been throughout March and April. There was a sharp rise on May 16th to the maximum size recorded (although possibly not the real maximum) for the year, followed by a sharp fall to June 13th as at other stations. After this the size altered little, only rising slightly in the end of July and beginning of August. The male follows the female curve fairly closely except that there was a marked decrease in size on August 8th. There was no maximum of size for males on July 11th as there was at the other stations.

The curves for Stage V show none of the variations characteristic of the other stations. The maximum size was found during the autumn and early winter when, as mentioned above, it remained very constant. The first brood was missed completely and after this there were only minor fluctuations which included a slight rise instead of a fall on June 13th. The size in September and October, 1932, was considerably less than in 1931. The Stage IV were measured only during the summer (May–October) and on the whole decreased from the beginning to the end of that period with no very marked variations.

At Station IV it is not so easy to connect periods of maximum size with the different broods. This is in the first place because measurements for the first brood have been missed entirely and, in the second, because there was a continuous production of eggs during March, April, and the beginning of May and it is difficult to be sure from which part of this breeding period any particular adults are derived. In the case of males and Stages V and IV there was no marked maximum or minimum of size at the coldest or warmest part of the year, but a gradual decline in size throughout the summer so that conditions in September, 1932, are quite different from those in 1931.

DISCUSSION.

If we consider the results as a whole we see that none of the three stations agrees exactly with any other although certain features are common to all. The median size curves of Stations I and II (Figs. 2 and 4), and to a less extent those of Station IV (Fig. 6), can be divided into three parts, each corresponding to one of the three breeding periods described in the preceding paper. At Station I the first appearance of the new brood a month after the egg maximum was marked by Calanus of large size, and the end of the brood, which was the time when most eggs were laid, was marked by Calanus of small size. This shows well for males, females, and Stage V and less clearly for Stage IV. At Station II the three groups can still be observed, but the beginning of the new brood was not marked by an increase in size although the end of the brood, and the egg laying period, were marked by a definite decrease. Although the three groups are not equally well defined in all stages, they are quite clear in females, and two of the groups are clear in males and Stage V. At Station IV the first group has been missed completely, the second is distinct, but the third, although probably present, is marked by no distinctive features.

The same changes are often found on the same date at different stations. Thus May 16th is a date when most of the Calanus at all stations were of large size, while on June 13th all stages of Calanus were of small size at all stations (except Stages V and IV at Station IV). A possible explanation of this might be that the population of Calanus as a whole had changed by migration. This is, however, negatived by several facts. Upper Loch Fyne (Station IV) shows in general the same size changes as the other stations, but cannot be subject to immigration since it is cut off from the rest of the area by two shallow bars. That it can develop and retain a plankton different from the rest of the area has already been shown (Marshall and Orr, 1927). Text-Figures 3 and 4 in the preceding paper indicate clearly that the Calanus population at Stations I and II also was stationary and that its development could be followed from month to month.

If then, as seems most probable, the Calanus of maximal and minimal size belong to the same brood (e.g. those of March 21st to April 18th ; and of May 16th to June 13th, etc.), it follows that the Calanus developed from eggs laid early in the breeding period are large and that those from eggs laid towards the end of it are small. The former holds good throughout the year only at Station I, but the latter is true in most cases. From the size measurements and times of egg production it would appear that the main mass of eggs is produced by Calanus of small size and that the large Calanus take little part in reproduction. This is probably not altogether true. The large females develop first, but since they wait for several weeks before laying eggs there is an accumulation of females and the smaller, later developed, females outnumber the early developed large ones, especially since these are all the time subject to processes of natural mortality. That large specimens are still present is seen in the size curves (Figs. 1, 3, and 5) where the increase and decrease of the median is shown to be caused more by the shifting of the mode than by alterations in the total range.

It might be supposed that the variations in size are caused by variations in the food supply, but observations on the microplankton do not bear this out (Fig. 2 in the preceding paper). Although at Station I the small Calanus of June 13th must have developed during a period of diatom poverty and the large specimens of May 16th and July 11th during a diatom-rich period, yet there are also many exceptions. The largest Calanus of all, those of March 21st, developed while diatoms were very scarce and the small specimens of July 25th developed while diatoms were comparatively abundant. At Station IV also the small Calanus of June 13th must have developed during that time of year when diatoms were richest in Loch Fyne and the largest, those of May 16th, when diatoms, although increasing, were not very numerous. Neither does the microplankton, apart from diatoms, show any relation to size.

Water temperatures were not taken regularly but can certainly not have been responsible for the size variations during the summer. The cause of the difference between Stage V Calanus at Station IV and those of the other stations may be the slightly lower temperature of the deep waters off Strachur during the summer and autumn. Mill (1891) has shown that this deep water is, owing to the contour of the bottom and the shallow bars cutting it off from lower Loch Fyne, so much isolated that the temperature lags behind that of the more open water of the area. From about June to December it is one or two degrees colder, and from February to April one or two degrees warmer than the deep water outside. No temperature measurements are available to explain the uniformity of sizes in the autumn of 1932.

During 1930–31 catches of Calanus were taken at Station I at irregular intervals with a stramin net, and samples were measured. It is interesting to note that the Stage V Calanus during the period April to September showed four distinct groups with maxima and minima at very much the same times as in 1932. There were maximal sizes at the beginning of April (when observations began), May 30th, July 12th, and August 15th, and minimal sizes on April 10th, June 10th, August 2nd, and September 16th. The resemblance is perhaps significant.

It seems as if the size variations were caused by some factor inherent in the method of reproduction of Calanus.

During most of the summer the catches were taken in two parts, one from the bottom to 30 m., the other from 30 m. to the surface. The adults, with one exception at each station, were never present in significantly large numbers above 30 m. On three occasions Stage V and on six occasions Stage IV were numerous enough to measure separately in the two catches. In every case with Stage V the Calanus from deep water were distinctly larger than those from the surface layers, the medians being respectively: May 30th, Station VI, 2.31 mm., 2·16 mm.; June 7th, Station I, 2·15 mm., 2·08 mm.; June 13th, Station II, (Fig. 7) (when there were more above than below 30 m.), 2·34 mm., 2·01 mm. Stage IV was also usually more abundant in water below 30 m., but on May 30th at Stations II and VI they were more numerous in the upper layers. On one occasion only, May 23rd at Station I, the larger specimens were found above 30 m. and the smaller below (median lengths 1·85 mm., 1·80 mm.), but as a rule the opposite was true, e.g. the median lengths of surface and deep water specimens respectively were: May 30th, Station I, 1·65 mm., 1·71 mm.; Station II (Fig. 7), 1·67 mm., 1·85 mm.; Station IV, 1·68 mm., 1·69 mm.; June 7th, Station I, 1·64 mm., 1·68 mm.; July 25th, Station II (Fig. 7), 1·63 mm., 1·73 mm.

As has been mentioned the Calanus from different stations also varied in size. During the autumn those from Station IV were larger (median length about 2·42 mm.) than those from Station II, and the latter (median length 2·12–2·27 mm.) were slightly larger than those from Station I (2·03–2·27 mm.). This distinction had been lost by the autumn of 1932. Several extra stations were worked quarterly and as a rule the sizes of Calanus at these stations differed little from those of the fortnightly stations nearest them. In August, however, Stage V and Stage IV Calanus from Station V, which is situated further up the main channel than Station I, were much smaller than any of the rest and were, in fact, the smallest found throughout the year.

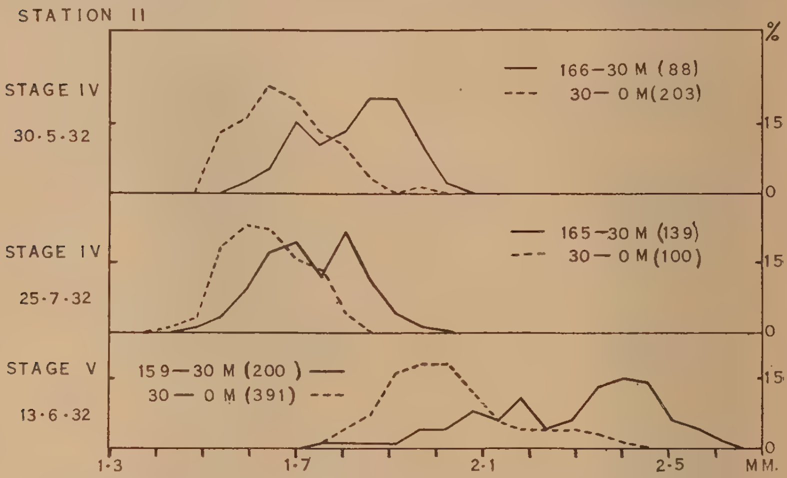

Fig. 7.—A comparison of the percentage size distribution of Stage IV and Stage V Calanus caught above and below 30 m. at Station II. The numbers for each haul are given in brackets.

One of the most striking features of the curves is the long range of sizes in almost every sample, a range almost as great as the whole yearly variation. Even when a large number of specimens is measured the curve does not lose its characteristic irregularity (Stage V : Station I, 30–10–32 ; Station II, 3-9-31, 22-8-32 ; Station IV, 13-6-32, 11-7-32). Although there is rarely any suggestion of two separate modes, yet such an irregular curve might be caused by the presence of two or more distinct forms or varieties whose sizes overlap.

Gurney (1929) and Sewell (1912, 1929, 1932) have both investigated numerous species of copepods in which the adult has a large size range, and have come to the conclusion that in many cases there are two forms of adult. Gurney assumes that there may be a second moult in the adult stage, while Sewell has put forward a more complicated scheme, in which the two adult forms, the " low " and the " high," are derived from Stages III, IV or V by moulting with appropriate growth factors. He comes to these conclusions mainly from a calculation of the growth factor (i.e. the proportion by which the length increases from one moult to the next), although there are also morphological differences between the " low " and " high " forms.

Now an examination of the curves in Figures 1, 3, and 5 would at first sight seem to support this. The curve for females always overlaps a large part of the curve for Stage V and occasionally (Station I, May 16th ; Station IV, August 8th) overlaps that for Stage IV too. The curve for males is also largely overlapped by that for Stage V and indeed the latter sometimes extends beyond it at the upper limit (Station I, April 18th ; Station II, September 5th ; Station IV, August 8th). It would therefore be quite possible for there to be two moults in either Stage V or Stage VI female, or for some Stage IV to moult directly into small females, the growth factor in these cases being one perfectly normal for copepods. Against this is the fact that the curves are never clearly bimodal and vary much from week to week. Also, if this kind of moult is as frequent as the curves suggest one would expect to find it in a fairly large percentage of cases, whereas although a large number of moulting Calanus have been observed, no abnormal moult has yet been seen.

Bogorov (1933) measured a number of all copepodite stages of *Calanus finmarchicus* from a tow netting taken in July, 1924, in the Barents Sea. He found that the size curves for Stages I, II, and III were unimodal, whereas those for Stages IV and V were bimodal, and he attributes this to the sex differentiation taking place in Stage IV. Males were not obtained but the curve for female sizes is very irregular and overlaps that for Stage V almost completely. The average size for females is actually smaller than that of Stage V and he attributes this to their belonging to a different brood. Another possibility is therefore that the small Stage V moult into males and the large into females. To test this a number of Stage V Calanus of different sizes was kept in separate beakers for about a fortnight (in autumn). Eight survived and moulted into adults. Of the large specimens (over 2·40 mm.) two became male and two female, and of the small (under 2·16 mm.) all four became female. It does not therefore appear that there is a sex differentiation in size in Stage V.

Gurney, however, has pointed out that the growth factor may change from moult to moult and is subject besides to much individual variation, facts which are borne out by the present investigation. If we consider all the adults as produced from the Stage V by a single moult (e.g. Station IV on June 13th, 1932, Fig. 5), it is obvious that they cannot all moult with even approximately the same growth factor. This, however, seems easier to believe than that there has been an abnormal moult in a large number of cases, since for that there is as yet no experimental evidence.

Some Calanus were kept separately in beakers to watch their growth, and measurements were made of the different stages (see the preceding paper, p. 91). When the growth factors are calculated it is found that there is a great deal of variation both from moult to moult in the same individual and also between individuals. Measurements made on living and active animals can of course be only approximate, but, for the moult from Stage V–Stage VI female, the factor varied from 1·06–1·21. The average factor was : Stage I–II (one case) 1·22, Stage II–III (seven cases) 1·22, Stage III–IV (thirteen cases) 1·19, Stage IV–V (thirteen cases) 1·17, Stage V–VI female (eleven cases) 1·12. Besides these specimens, which were examined especially for their development, a large number has been kept for other purposes and in no case has any but a normal moult been observed. Until some experimental evidence has been obtained the suggestions of Gurney and Seymour Sewell must remain only possibilities.

Sewell's copepods were mostly taken from brackish water at river mouths and these peculiar conditions may have affected their development, but Gurney worked on freshwater copepods from lakes in different parts of the world.

A long and irregular range of sizes may be caused, not by dimorphism in one stage or another, but by a mixture of races or varieties. Such a curve (with a range of only 0·55 mm.) has been shown by Steuer (1925) for *Pleuromamma gracilis* to be composed of three different races, characterised by slight morphological differences as well as by varying size. In his cases, however, the different varieties were usually found in different parts of the geographical range, or, if caught at the same station, could be assumed to inhabit different depths. Such an explanation would not hold with Calanus in the present case.

Calanus of varying sizes in the same catch have already been described by Leif Störmer (1929) from the west coast of Greenland, and by Ottestad (1932) from Antarctic seas. In the latter case the water mass being sampled was composed of water of several origins and the irregularities in the size curves of the Calanus (*C. acutus* and *C. propinquus*) are explained as having been caused by the Calanus belonging to these different water masses and having different developmental histories. Off the west coast of Greenland there are two distinct sizes of Calanus, a large and a small, and Störmer finds that whereas the small form is the product of the same year's growth, the large form has survived a winter and is really more than one year old. There is no evidence that in the Clyde we are dealing with anything but a homogeneous mass of water, and the Calanus in it are certainly never more than a few months old, so that neither of these explanations can hold good here.

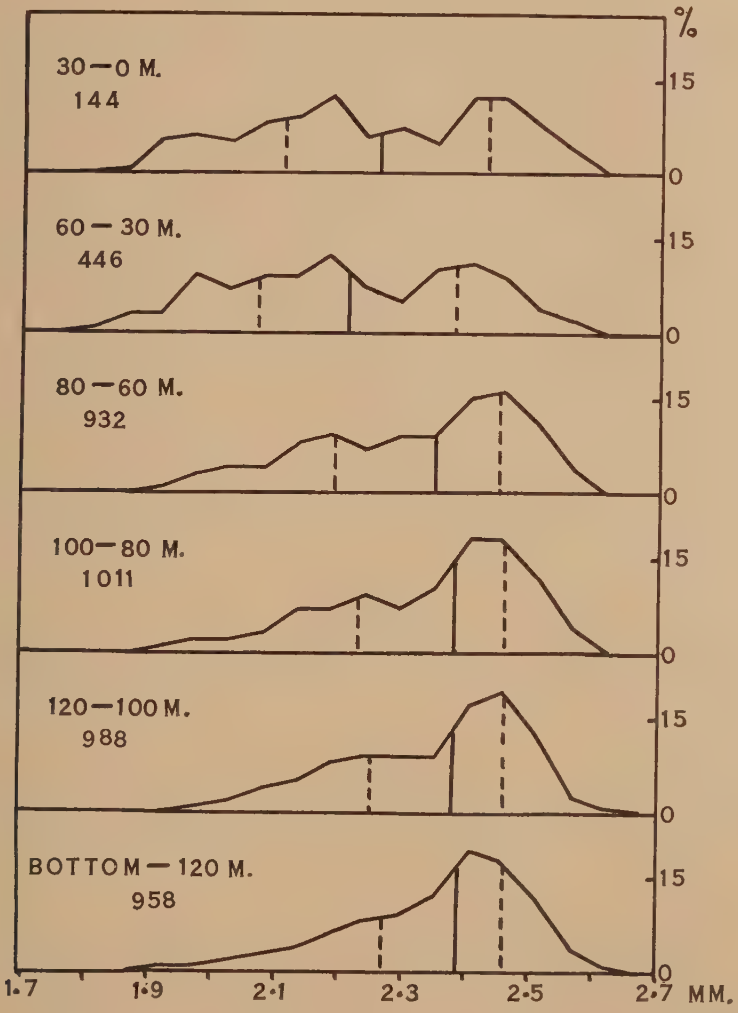

Fig. 8.—The percentage size distribution of Calanus from different depths at Station IV on January 25th–26th, 1932. The position of the first and third quartiles is marked with vertical broken lines and that of the second quartile (median) with a continuous vertical line. The numbers measured for each depth are given below the depth.

Russell (1928) has suggested that there may be a segregation of broods in different water layers, the small summer brood living nearer the surface than the large winter brood. As we have seen, during the summer (May–July) the Calanus near the surface (above 30 m.) were distinctly smaller than those from deep water. During at least the early part of this period there may have been a mixture of broods present and an examination was therefore made of the sizes of Stage V at different depths in Loch Fyne in January. At this time the population of Calanus is homogeneous, breeding has not yet begun, and all the Stage V present have survived the winter as such and are the product of the late summer broods.

On January 25–26th, a vertical distribution station was worked by Dr. A. G. Nicholls and samples are available at 20-metre depths from the bottom up to 60 m., as well as from 60–30 m. and 30 m. to the surface. Samples from all these depths were measured and it was found (Fig. 8) that in every case the samples above 60 m. contained a larger proportion of small specimens than those from below. Below 60 m. there was little difference between any of the samples. These results indicate that even in a homogeneous population the small specimens of Calanus tend to be found nearer the surface than the large. This confirms Gardiner's (1933) recent observations on Calanus in the North Sea. An examination and comparison of a small and a large Calanus showed no significant morphological differences, and the tendency can perhaps be regarded as the first step in the process which Steuer has studied, the process by which a small, surface-living variety becomes separated off from a larger deep water species.

SUMMARY.

The size of the cephalothorax in Stage IV, Stage V, and Stage VI Calanus has been measured during the year 1931–1932 at three stations in the Clyde Sea-Area.

In general the size was greatest when the water temperature was low, and least when it was high, but besides this there was a series of increases and decreases in size which were apparently connected with the breeding periods. The Calanus produced at the beginning of a breeding period were large (at Station I) and those produced at the end were small (at Stations I and II). The greatest production of eggs usually occurred when the female Calanus were of small size.

During the autumn of 1931 the Stage V Calanus from Station IV (upper Loch Fyne) were considerably larger than those from the rest of the area, but this distinction had been lost by the autumn of 1931.

Stages IV and V Calanus taken in the top 30 m. were almost invariably smaller than those from deeper water.

The Calanus show a very wide range of sizes, the range for Stage V overlapping those for both male and female. Possible causes of this are discussed.

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TABLES I–IV.

Measurements of Carapace-Length in mm. The measurements were made with an eye-piece micrometer of which one division = 0·054 mm. The figures in ordinary type are the actual numbers found; the figures in italics are percentages.

TABLE I.

MALES. LENGTH OF CARAPACE IN MM.

Station.	Date	1·944–1·998	1·998–2·052	2·052–2·106	2·106–2·160	2·160–2·214	2·214–2·268	2·268–2·322	2·322–2·376	2·376–2·430	2·430–2·484	2·484–2·538	2·538–2·592	2·592–2·646	2·646–2·700	2·700–2·754	2·754–2·808	2·808–2·862	Number measured.	Median length
I	21-3-32								2 *3*	3 *4*	11 *14*	34 *44*	21 *27*	5 *6*	2 *3*				78	2·522
,,	28-3-32							1 *1*	2 *2*	8 *8*	20 *21*	36 *38*	22 *23*	6 *6*					95	2·510
,,	5-4-32					1 *1*	2 *3*	7 *10*	5 *7*	7 *10*	16 *22*	10 *14*	18 *25*	5 *7*	2 *3*				73	2·481
,,	18-4-32					1 *3*	4 *11*	4 *11*	3 *8*	13 *36*	9 *25*	2 *5*							36	2·403
,,	27-4-32				1 *6*	– –	– –	2 *12*	3 *19*	4 *25*	5 *31*	1 *6*							16	2·410
,,	2-5-32					1 *5*	– –	2 *9*	5 *23*	6 *27*	7 *32*	– –	1 *5*						22	2·408
,,	16-5-32					1	–	–	4	2	2	–	2						11	2·403
,,	23-5-32								2 *8*	7 *27*	4 *15*	4 *15*	3 *12*	2 *8*	3 *12*	– –	1 *4*		26	2·491
,,	7-6-32						1 *3*	2 *5*	5 *13*	4 *10*	5 *13*	4 *10*	8 *21*	4 *10*	5 *13*	– –	1 *3*		39	2·525
,,	27-6-32				2 *2*	1 *1*	9 *9*	21 *21*	11 *11*	14 *14*	11 *11*	12 *12*	7 *7*	5 *5*	2 *2*	5 *5*	1 *1*		101	2·403
,,	11-7-32				1 *1*	– –	2 *2*	2 *2*	4 *4*	8 *8*	14 *14*	21 *21*	19 *19*	16 *16*	7 *7*	4 *4*			98	2·532
,,	25-7-32	1 *1*	– –	1 *1*	6 *9*	6 *9*	14 *21*	8 *12*	4 *6*	9 *13*	4 *6*	8 *12*	2 *3*	3 *4*	2 *3*				68	2·312
,,	8-8-32				3 *6*	4 *8*	5 *10*	5 *10*	5 *10*	5 *10*	9 *17*	4 *8*	3 *6*	3 *6*	4 *8*	2 *4*			52	2·425
,,	22-8-32							4 *21*	6 *32*	6 *32*	1 *5*	1 *5*	– –	1 *5*					19	2·376
,,	5-9-32						1 *4*	2 *8*	8 *33*	10 *42*	1 *4*	2 *8*							24	2·384
II	11-1-32									2 *8*	3 *12*	5 *20*	9 *36*	4 *16*	1 *4*	1 *4*			25	2·556
,,	25-1-32						1 *2*	– –	2 *4*	9 *19*	10 *21*	7 *15*	11 *23*	7 *15*	1 *2*				48	2·503
,,	8-2-32						1 *1*	4 *5*	6 *8*	9 *12*	11 *15*	21 *28*	16 *21*	4 *5*	2 *3*	– –	1 *1*		75	2·502

,,	5-4-32						1 *2*	1 *2*	6 *10*	12 *20*	17 *29*	14 *24*	6 *10*	1 *2*	1 *2*				59	2·462
,,	2-5-32				1 *1*	– *–*	5 *4*	7 *6*	20 *17*	33 *28*	21 *18*	18 *15*	9 *8*	3 *3*					117	2·419
,,	16-5-32							1 *4*	1 *4*	6 *23*	8 *31*	5 *19*	2 *8*	2 *8*	1 *4*				26	2·467
,,	13-6-32	1 *6*	– *–*	1 *6*	– *–*	– *–*	5 *29*	3 *18*	1 *6*	1 *6*	2 *12*	1 *6*	1 *6*	– *–*	– *–*	1 *6*			17	2·304
,,	27-6-32		1 *4*	– *–*	4 *16*	– *–*	1 *4*	1 *4*	5 *20*	3 *12*	2 *8*	2 *8*	2 *8*	3 *12*	1 *4*				25	2·394
,,	11-7-32							1 *2*	2 *4*	5 *10*	6 *13*	10 *21*	9 *19*	8 *17*	6 *13*	1 *2*			48	2·541
,,	8-8-32	1 *2*	– *–*	1 *2*	6 *10*	5 *8*	6 *10*	14 *22*	6 *10*	10 *16*	8 *13*	3 *5*	1 *2*	2 *3*					63	2·318
,,	5-9-32					1 *3*	6 *15*	8 *20*	16 *40*	6 *15*	3 *8*								40	2·341
IV	25-1-32									3 *6*	6 *12*	13 *25*	15 *29*	9 *18*	4 *8*	1 *2*			51	2·552
,,	25-26-1-32						5 *–*	8 *1*	37 *3*	85 *7*	180 *14*	299 *23*	354 *27*	217 *17*	95 *7*	16 *1*	2 *–*		1298	2·543
,,	8-2-32					1 *1*	– *–*	– *–*	3 *2*	8 *6*	12 *9*	28 *22*	41 *32*	21 *16*	11 *9*	3 *2*			128	2·555
,,	22-2-32									1 *1*	11 *11*	18 *18*	29 *28*	29 *28*	11 *11*	3 *3*			102	2·578
,,	7-3-32									4 *9*	4 *9*	7 *16*	10 *23*	10 *23*	7 *16*	1 *2*			43	2·576
,,	2-5-32							2 *8*	2 *8*	5 *19*	4 *15*	7 *27*	3 *12*	3 *12*					26	2·488
,,	16-5-32							4 *3*	7 *5*	22 *17*	24 *18*	33 *25*	19 *15*	13 *10*	5 *4*	1 *1*	1 *1*	1 *1*	130	2·498
,,	30-5-32							3 *16*	2 *11*	4 *21*	5 *26*	1 *5*	2 *11*	3 *16*					19	2·441
,,	13-6-32				1 *2*	– *–*	4 *8*	4 *8*	9 *18*	11 *22*	9 *18*	5 *10*	5 *10*	– *–*	1 *2*				49	2·410
,,	27-6-32				2 *1*	2 *1*	9 *6*	13 *9*	29 *19*	29 *19*	19 *13*	15 *10*	18 *12*	8 *5*	5 *3*				149	2·413
,,	11-7-32					2 *4*	5 *10*	2 *4*	11 *22*	8 *16*	11 *22*	4 *8*	4 *8*	2 *4*					49	2·410
,,	5-7-32					1 *2*	5 *11*	2 *4*	4 *9*	16 *36*	8 *18*	5 *11*	4 *9*						45	2·413
,,	8-8-32			1 *5*	3 *14*	– *–*	4 *19*	– *–*	6 *29*	1 *5*	3 *14*	3 *14*							21	2·349
,,	5·9-32					2	3	1	3										9	2·322

TABLE II.

FEMALES. LENGTH OF CARAPACE IN MM.

Station	Date.	1·944–1·998	1·998–2·052	2·052–2·106	2·106–2·160	2·160–2·214	2·214–2·268	2·268–2·322	2·322–2·376	2·376–2·430	2·430–2·484	2·484–2·538	2·538–2·592	2·592–2·646	2·646–2·700	2·700–2·754	2·754–2·808	2·808–2·862	2·862–2·916	2·916–2·970	2·970–3·024	Number measured.	Median length
I	22-2-32					2 *4*	2 *4*	2 *4*	7 *13*	11 *21*	5 *9*	10 *19*	5 *9*	4 *8*	4 *8*	– –	1 *2*					53	2·462
,,	21-3-32						1 *2*	– –	2 *4*	1 *2*	2 *4*	2 *4*	2 *4*	5 *10*	7 *13*	4 *8*	15 *29*	6 *12*	3 *6*	1 *2*	1 *2*	52	2·756
,,	28-3-32									3 *4*	– –	2 *3*	2 *3*	6 *8*	16 *22*	18 *25*	14 *19*	1 *14*	*1*	1 *1*		73	2·724
,,	5-4-32						1 *1*	– –	– –	6 *8*	8 *10*	6 *8*	8 *10*	7 *9*	10 *13*	14 *18*	9 *11*		*4*	1 *1*	1 *1*	80	2·670
,,	18-4-32				1 *1*	– –	1 *1*	2 *2*	4 *5*	6 *7*	10 *12*	9 *11*	12 *14*	9 *11*	11 *13*	11 *13*	4 *5*	2 *2*	2 *2*	– –	1 *1*	85	2·583
,,	27-4-32					1 *2*	1 *2*	1 *2*	4 *9*	8 *18*	4 *9*	7 *16*	8 *18*	6 *14*	1 *2*	2 *5*	1 *2*					44	2·511
,,	2-5-32						1 *1*	– –	2 *2*	6 *6*	13 *13*	24 *24*	23 *23*	12 *12*	9 *9*	4 *4*	3 *3*	1 *1*	1 *1*			99	2·547
,,	16-5-32		1 *1*	– –	1 *1*	1 *1*	– –	– –	3 *2*	3 *2*	14 *11*	15 *12*	19 *15*	19 *15*	20 *16*	21 *17*	1 *1*	3 *2*	2 *2*	– –	1 *1*	124	2·608
,,	23-5-32								5 *3*	11 *6*	16 *9*	31 *18*	34 *20*	31 *18*	23 *13*	15 *9*	4 *2*	3 *2*				173	2·576
,,	30-5-32								1 *2*	7 *13*	12 *22*	10 *19*	7 *13*	6 *11*	6 *11*	4 *7*	1 *2*					54	2·525
,,	7-6-32							1 *1*	2 *2*	10 *9*	16 *15*	17 *16*	26 *24*	18 *17*	10 *9*	3 *3*	2	2 *2*	2 *2*			109	2·557
,,	13-6-32					1 *8*	– –	1 *8*	4 *31*	2 *15*	1 *8*	2 *15*	1 *8*	– –	– –	1 *8*						13	2·403
,,	27-6-32					5 *3*	11 *6*	26 *14*	27 *15*	41 *22*	34 *19*	20 *11*	10 *5*	2 *1*	3 *2*	4 *2*						183	2·406
,,	11-7-32						14 *5*	20 *7*	33 *12*	51 *18*	52 *19*	38 *14*	32 *11*	16 *6*	17 *6*	7 *2*	1 –					281	2·450
,,	25-7-32		1 *1*	1 *1*	3 *3*	14 *13*	22 *21*	13 *12*	12 *11*	17 *16*	8 *7*	7 *7*	2 *2*	2 *2*	4 *4*	1 *1*						107	2·322
,,	8-8-32			3 *3*	1 *1*	8 *8*	17 *17*	10 *10*	19 *19*	17 *17*	9 *9*	8 *8*	3 *3*	2 *2*	– –	– –	2 *2*					99	2·353
,,	22-8-32				2 *6*	– –	3 *8*	2 *6*	3 *8*	6 *17*	7 *19*	9 *25*	4 *11*									36	2·449
,,	5-9-32				1 *2*	3 *6*	5 *9*	3 *6*	5 *9*	10 *19*	9 *17*	11 *21*	3 *6*	1 *2*	2 *4*							53	2·430
,,	30-10-32								1	1	–	–	1	3	2	3						11	2·646
II	3-9-31					1 *5*	1 *5*	2 *10*	1 *5*	4 *20*	1 *5*	4 *20*	3 *15*	3 *15*								20	2·491
,,	8-2-32				1 *2*	– –	– –	4 *7*	8 *15*	13 *24*	8 *15*	11 *20*	5 *9*	2 *4*	1 *2*	1 *2*						54	2·440
,,	22-2-32						2 *6*	3 *9*	2 *6*	4 *11*	4 *11*	6 *17*	10 *29*	2 *6*	– –	2 *6*						35	2·511
,,	5-4-32								3 *5*	3 *5*	8 *14*	3 *5*	7 *12*	7 *12*	7 *12*	8 *14*	10 *17*	2 *3*	1 *2*			59	2·638

,,	2-5-32						1	2	10	8	10	31	26	20	15	10	6	2				141	2·556
							1	*1*	*7*	*6*	*7*	*22*	*18*	*14*	*11*	*7*	*4*	*1*					
,,	16-5-32									2	7	11	8	3	5	2	2	1	1			42	2·548
										5	*17*	*26*	*19*	*7*	*12*	*5*	*5*	*2*	*2*				
,,	30-5-32							3	7	10	20	19	33	24	21	13	5	1	1	1	1	159	2·572
								2	*4*	*6*	*13*	*12*	*21*	*15*	*13*	*8*	*3*	*1*	*1*	*1*	*1*		
,,	13-6-32			1	3	8	14	12	13	17	16	8	21	22	10	1	5	2	–	1		154	2·462
				1	*2*	*5*	*9*	*8*	*8*	*11*	*10*	*5*	*14*	*14*	*6*	*1*	*3*	*1*	–	*1*			
,,	27-6-32					1	1	4	8	8	5	7	3	5	4	2	1	1				50	2·468
						2	*2*	*8*	*16*	*16*	*10*	*14*	*6*	*10*	*8*	*4*	*2*	*2*					
,,	11-7-32					3	4	13	12	16	27	21	22	13	2	4	1	1				139	2·474
						2	*3*	*9*	*9*	*12*	*19*	*15*	*16*	*9*	*1*	*3*	*1*	*1*					
,,	25-7-32		1	–	–	3	1	3	2	7	4	7	6	1	1	2	–	1				39	2·471
			3	–	–	*8*	*3*	*8*	*5*	*18*	*10*	*18*	*15*	*3*	*3*	*5*	–	*3*					
,,	8-8-32		2	1	10	12	14	21	23	35	23	29	11	15	8	2	2					208	2·409
			1	–	*5*	*6*	*7*	*10*	*11*	*17*	*11*	*14*	*5*	*7*	*4*	*1*	*1*						
,,	22-8-32			2	1	1	3	2	5	3	3	3	2	1	2							28	2·385
				7	*4*	*4*	*11*	*7*	*18*	*11*	*11*	*11*	*7*	*4*	*7*								
,,	5-9-32				1	5	7	9	19	23	11	13	7	2	1	1	3					102	2·401
					1	*5*	*7*	*9*	*19*	*23*	*11*	*13*	*7*	*2*	*1*	*1*	*3*						
,,	30-10-32										1	2	6	4	3	–	1	1				18	2·599
											6	*11*	*33*	*22*	*17*	–	*6*	*6*					
IV	25-26-1-32				1	2	4	10	16	23	36	43	24	22	18	6	8	2				215	2·504
					–	*1*	*2*	*5*	*7*	*11*	*17*	*20*	*11*	*10*	*8*	*3*	*4*	*1*					
,,	8-2-32					2	4	4	8	8	16	18	12	17	13	9	5	2				118	2·536
						2	*3*	*3*	*7*	*7*	*14*	*15*	*10*	*14*	*11*	*8*	*4*	*2*					
,,	22-2-32							3	–	1	7	2	6	2	6	1	–	1				29	2·556
								10	–	*3*	*24*	*7*	*21*	*7*	*21*	*3*	–	*3*					
,,	7-3-32							1	1	2	3	6	5	5	6	4	4	2	1	1		41	2·624
								2	*2*	*5*	*7*	*15*	*12*	*12*	*15*	*10*	*10*	*5*	*2*	*2*			
,,	2-5-32							1	3	3	9	32	36	30	20	23	11	2	1	1		172	2·597
								1	*2*	*2*	*5*	*19*	*21*	*17*	*12*	*13*	*6*	*1*	*1*	*1*			
,,	16-5-32								1	2	6	8	17	27	35	29	19	12	6	1	2	165	2·680
									1	*1*	*4*	*5*	*10*	*16*	*21*	*18*	*12*	*7*	*4*	*1*	*1*		
,,	30-5-32						1	–	–	2	4	1	2	2	3	–	2	–	1			18	2·579
							6	–	–	*11*	*22*	*6*	*11*	*11*	*17*	–	*11*	–	*6*				
,,	13-6-32					3	10	16	34	26	24	19	11	7	6	2	1	1				161	2·413
						2	*6*	*10*	*21*	*16*	*15*	*12*	*7*	*4*	*4*	*1*	*1*	*1*					
,,	27-6-32				2	2	19	31	43	35	50	36	20	15	7	1	3	1				265	2·431
					1	*1*	*7*	*12*	*16*	*13*	*19*	*14*	*8*	*6*	*3*	–	*1*	–					
,,	11-7-32			1	2	7	9	21	35	31	19	23	15	11	13	3	3	1				194	2·415
				1	*1*	*4*	*5*	*11*	*18*	*16*	*9*	*12*	*8*	*6*	*7*	*2*	*2*	*1*					
,,	11-12-7-32			2	1	10	16	38	49	43	46	27	20	9	8	3	1					273	2·402
				1	–	*4*	*6*	*14*	*18*	*16*	*17*	*10*	*7*	*3*	*3*	*1*	–						
,,	25-7-32		1	–	–	4	4	11	11	13	19	15	6	6	3	3						96	2·443
			1	–	–	*4*	*4*	*11*	*11*	*14*	*20*	*16*	*6*	*6*	*3*	*3*							
,,	8-8-32	1	1	4	4	12	11	13	19	10	33	23	15	8	10	7	1	1	2			175	2·451
		1	*1*	*2*	*2*	*7*	*6*	*7*	*11*	*6*	*19*	*13*	*9*	*5*	*6*	*4*	*1*	*1*	*1*				
,,	22-8-32			2	7	5	8	9	8	11	16	10	16	6	3	4	4	2	–	1		112	2·452
				2	*6*	*4*	*7*	*8*	*7*	*10*	*14*	*9*	*14*	*5*	*3*	*4*	*4*	*2*	–	*1*			
,,	5-9-32			3	4	6	9	10	7	10	8	9	7	3	6	2	–	1				85	2·398
				4	*5*	*7*	*11*	*12*	*8*	*12*	*9*	*11*	*8*	*4*	*7*	*2*	–	*1*					

TABLE III.

STAGE V. LENGTH OF CARAPACE IN MM.

Station.	Date.	1·674-1·728	1·728–1·782	1·782 1·836	1·836–1·890	1·890–1·944	1·944–1·998	1·998–2·052	2·052–2·106	2·106–2·160	2·160–2·214	2·214–2 268	2·268–2·322	2·322–2·376	2·376–2·430	2·430–2·484	2·484–2·538	2·538–2·592	2·592–2·646	2·646–2·700	2·700–2·754	Number measured.	Median length.
I	3-9-31				7 *3*	14 *6*	27 *12*	26 *12*	20 *9*	19 *9*	14 *6*	24 *11*	25 *11*	19 *9*	15 *7*	9 *4*	4 *2*					223	2·157
,,	15-9-31			2 *3*	2 *3*	8 *12*	14 *21*	12 *18*	6 *9*	2 *3*	5 *7*	9 *13*	4 *6*	3 *4*	– *–*	– *–*	– *–*	– *–*	1 *1*			68	2·036
,,	21-10-31		1 *1*	2 *2*	6 *5*	14 *11*	19 *15*	8 *6*	13 *10*	7 *6*	17 *14*	15 *12*	9 *7*	3 *2*	5 *4*	5 *4*						124	2·104
,,	16-11-31				3 *2*	5 *4*	8 *7*	14 *11*	13 *11*	11 *9*	10 *8*	12 *10*	10 *8*	10 *8*	12 *10*	11 *9*	3 *2*	1 *1*				123	2·203
,,	30-11-31				1 *1*	3 *4*	2 *3*	3 *4*	7 *9*	5 *6*	12 *16*	5 *6*	11 *14*	5 *6*	7 *9*	9 *12*	5 *6*	2 *3*				77	2·273
,,	11-1-32					2 *5*	3 *8*	2 *5*	7 *19*	4 *11*	3 *8*	4 *11*	3 *8*	1 *3*	2 *5*	6 *16*						37	2·178
,,	21-3-32						2 *1*	2 *1*	1 *1*	3 *2*	12 *7*	30 *17*	41 *24*	45 *26*	28 *16*	7 *4*	3 *2*					174	2·318
,,	28-3-32							1 *–*	7 *2*	16 *5*	33 *10*	45 *13*	50 *15*	74 *22*	74 *22*	28 *8*	11 *3*	4 *1*	*1* –			344	2·337
,,	5-4-32					1 *1*	4 *2*	8 *4*	10 *6*	11 *6*	23 *13*	28 *15*	39 *22*	24 *13*	12 *7*	14 *8*	5 *3*	1 *1*	1 *1*			181	2·276
,,	18-4-32				3 *2*	3 *2*	10 *6*	15 *8*	27 *15*	20 *11*	14 *8*	22 *12*	15 *8*	20 *11*	15 *8*	9 *5*	4 *2*	2 *1*	1 *1*			180	2·208
,,	27-4-32				1 *1*	1 *1*	4 *4*	7 *7*	14 *15*	13 *14*	7 *7*	8 *8*	5 *5*	11 *12*	16 *17*	7 *7*	1 *1*					95	2·221
,,	2-5-32						1 *1*	– *–*	2 *2*	11 *9*	12 *10*	9 *8*	12 *10*	15 *13*	25 *21*	18 *15*	9 *8*	4 *3*				118	2·367
,,	16-5-32								1 *1*	4 *5*	10 *12*	4 *5*	3 *4*	6 *7*	17 *20*	15 *18*	10 *12*	8 *10*	4 *5*	2 *2*		84	2·422
,,	23-5-32							6 *2*	10 *4*	20 *8*	25 *10*	25 *10*	28 *11*	35 *14*	34 *14*	34 *14*	17 *7*	11 *4*	3 *1*			248	2·338
,,	30-5-32						4 *7*	4 *7*	2 *3*	5 *8*	9 *15*	5 *8*	6 *10*	5 *8*	7 *11*	4 *7*	5 *8*	5 *8*				61	2·286
,,	7-6-32		3 *1*	– *–*	*–*	8 *3*	17 *6*	29 *10*	50 *17*	60 *20*	36 *12*	19 *6*	27 *9*	11 *4*	15 *5*	14 *5*	5 *2*	5 *2*	2 *1*			118–30 m. 301 ($\frac{1}{5}$)	2·146
,,	,,					3 *10*	7 *23*	3 *10*	5 *17*	8 *27*	1 *3*	– *–*	1 *3*	1 *3*	– *–*	1 *3*						30–0 m. 30	2·079
,,	,,		15 *1*	– *–*	– *–*	43 *3*	92 *6*	143 *9*	255 *17*	308 *20*	161 *10*	95 *6*	136 *9*	56 *4*	75 *5*	71 *5*	25 *2*	25 *2*	10 *1*			118–0 m. (calc.) 1536	2·144
,,	13-6-32			2 *2*	1 *1*	5 *4*	12 *11*	13 *12*	17 *15*	20 *18*	13 *12*	9 *8*	10 *9*	3 *3*	3 *3*	3 *3*	– *–*	– *–*	– *–*	1 *1*		112	2·124
,,	27-6-32					3 *3*	10 *9*	11 *10*	5 *5*	12 *11*	9 *8*	18 *17*	19 *18*	7 *7*	9 *8*	4 *4*	– *–*	1 *1*				107	2·226
,,	11-7-32					6 *3*	11 *5*	17 *7*	27 *11*	25 *10*	18 *8*	26 *11*	22 *9*	26 *11*	26 *11*	23 *10*	10 *4*	2 *1*	1 *–*			240	2·248
,,	25-7-32		1 *–*	9 *3*	18 *6*	40 *14*	44 *16*	37 *13*	40 *14*	30 *11*	10 *3*	17 *6*	12 *4*	12 *4*	4 *1*	1 *–*	3 *1*					278	2·038
,,	8-8-32				1 *2*	– *–*	7 *13*	11 *20*	6 *11*	5 *9*	2 *4*	9 *16*	8 *15*	5 *9*	1 *2*							55	2·138

,,	22-8-32		3 *1*	8 *4*	22 *10*	28 *12*	24 *11*	26 *12*	24 *11*	15 *7*	23 *10*	25 *11*	16 *7*	7 *3*	3 *1*	2 *1*						225	2·057
,,	5-9-32			7 *3*	7 *3*	32 *14*	35 *16*	39 *18*	24 *11*	9 *4*	13 *6*	17 *8*	17 *8*	13 *6*	6 *3*	2 *1*						221	2·040
,,	30-10-32			2 *1*	5 *2*	15 *5*	11 *4*	17 *6*	20 *7*	18 *6*	24 *8*	35 *12*	26 *9*	17 *6*	24 *8*	38 *12*	33 *11*	17 *6*	1 *–*	1 *–*		304	2·279
II	3-9-31			1 *–*	10 *3*	25 *8*	44 *13*	50 *15*	29 *9*	31 *9*	31 *9*	29 *9*	18 *5*	22 *7*	20 *6*	14 *4*	2 *1*	2 *1*				328	2·116
,,	15-9-31			2 *2*	2 *2*	6 *5*	10 *8*	12 *10*	14 *11*	13 *11*	17 *14*	8 *7*	8 *7*	9 *7*	13 *11*	5 *4*	4 *3*					123	2·170
,,	1-10-31					3 *2*	10 *8*	8 *6*	9 *7*	13 *10*	14 *11*	15 *11*	10 *8*	7 *5*	19 *14*	15 *11*	6 *5*	2 *2*	1 *1*			132	2·248
,,	21-10-31					1 *1*	6 *5*	6 *5*	11 *9*	11 *9*	14 *12*	8 *7*	7 *6*	15 *12*	18 *15*	13 *11*	6 *5*	4 *3*				120	2·295
,,	5-11-31				2 *1*	7 *5*	5 *4*	19 *14*	15 *11*	13 *10*	16 *12*	11 *8*	11 *8*	9 *7*	11 *8*	10 *7*	2 *1*	1 *1*	2 *1*			134	2·182
,,	16-11-31				1 *1*	3 *3*	9 *9*	10 *10*	6 *6*	12 *11*	11 *11*	9 *9*	9 *9*	5 *5*	15 *14*	8 *8*	3 *3*	2 *2*				103	2·214
,,	30-11-31				1 *1*	1 *1*	7 *5*	8 *6*	6 *4*	15 *11*	20 *15*	16 *12*	14 *10*	12 *9*	13 *10*	8 *6*	8 *6*	5 *4*	– *–*	1 *1*		135	2·248
,,	14-12-31			1 *1*	1 *1*	5 *4*	8 *6*	14 *11*	8 *6*	8 *6*	8 *6*	11 *9*	13 *10*	17 *13*	11 *9*	16 *12*	7 *5*	– *–*	1 *1*			129	2·272
,,	30-12-31				1 *1*	1 *1*	3 *2*	13 *9*	12 *8*	14 *10*	21 *15*	13 *9*	4 *3*	14 *10*	16 *11*	21 *15*	7 *5*	2 *1*	1 *1*			143	2·243
,,	11-1-32				1 *1*	– *–*	5 *4*	10 *8*	12 *9*	12 *9*	12 *9*	15 *12*	12 *9*	6 *5*	13 *10*	20 *16*	9 *7*	2 *2*				129	2·261
,,	25-1-32					2 *2*	5 *4*	16 *12*	12 *9*	14 *11*	19 *14*	20 *15*	15 *11*	12 *9*	6 *5*	8 *6*	3 *2*					132	2·210
,,	8-2-32				2 *5*	2 *5*	3 *7*	3 *7*	5 *12*	6 *14*	7 *17*	5 *12*	3 *7*	3 *7*	1 *2*	1 *2*	– *–*	– *–*	– *–*	1 *2*		42	2·164
,,	21-3-32								1 *4*	1 *4*	3 *12*	10 *40*	4 *16*	2 *8*	3 *12*	– *–*	1 *4*					25	2·257
,,	5-4-32					2 *1*	4 *3*	1 *1*	12 *8*	12 *8*	26 *18*	31 *22*	23 *16*	15 *10*	10 *7*	8 *6*						144	2·240
,,	2-5-32					1 *–*	3 *1*	2 *1*	1 *–*	5 *2*	22 *10*	10 *4*	18 *8*	32 *14*	48 *22*	36 *16*	35 *16*	8 *4*	1 *–*	1 *–*		223	2·396
,,	16-5-32						2 *2*	– *–*	6 *7*	9 *10*	11 *13*	6 *7*	8 *9*	5 *6*	13 *15*	14 *16*	8 *9*	4 *5*				86	2·338
,,	30-5-32								10 *6*	12 *7*	15 *9*	20 *12*	11 *7*	17 *10*	30 *18*	25 *15*	17 *10*	4 *2*	1 *1*	– *–*	1 *1*	163	2 366
,,	13-6-32		1 *1*	2 *1*	2 *1*	2 *1*	8 *4*	8 *4*	17 *8*	12 *6*	21 *11*	8 *4*	13 *6*	26 *13*	29 *15*	28 *14*	12 *6*	9 *4*	2 *1*			159–30 m. 200	2·336
,,	,,	1 *–*	5 *1*	14 *4*	29 *7*	63 *16*	71 *18*	71 *18*	47 *12*	25 *6*	15 *4*	16 *4*	17 *4*	10 *3*	4 *1*	2 *–*	1 *–*					30–0 m. 391	2·008
,,	,,	1 *–*	6 *1*	16 *3*	31 *5*	65 *11*	79 *13*	79 *13*	64 *11*	37 *6*	36 *6*	24 *4*	30 *5*	36 *6*	33 *6*	30 *5*	13 *2*	9 *2*	2 *–*			159–0 m. 591	2·068
,,	27-6-32				2 *1*	1 *–*	11 *5*	9 *4*	23 *11*	14 *7*	19 *9*	12 *6*	13 *6*	23 *11*	31 *15*	24 *12*	16 *8*	4 *2*				202	2·312
,,	11-7-32					3 *1*	10 *4*	25 *9*	20 *8*	27 *10*	19 *7*	26 *9*	26 *9*	29 *11*	21 *8*	35 *13*	16 *6*	5 *2*	2 *1*	1 *–*		265	2·274
,,	25-7-32		1 *–*	1 *–*	6 *2*	10 *3*	10 *3*	24 *7*	33 *10*	38 *12*	24 *7*	18 *6*	30 *9*	26 *8*	34 *11*	23 *7*	9 *3*	8 *2*	1 *–*	– *–*	1 *–*	297	2·216
,,	8-8-32			3 *1*	5 *2*	13 *4*	31 *11*	37 *13*	30 *10*	26 *9*	23 *8*	35 *12*	22 *8*	15 *5*	21 *7*	19 *7*	9 *3*	2 *1*				291	2·162
,,	22-8-32		1 *–*	2 *1*	10 *3*	13 *4*	43 *14*	41 *13*	37 *12*	83 *11*	16 *5*	29 *9*	28 *9*	23 *7*	19 *6*	12 *4*	3 *1*	– *–*	1 *–*			311	2·121

TABLE III—(*continued*).

Station.	Date.	1·674– 1·728	1·728– 1·782	1·782– 1·836	1·836– 1·890	1·890– 1·944	1·944– 1·998	1·998– 2·052	2·052– 2·106	2·106– 2·160	2·160 2·214	2·214– 2·268	2·268– 2·322	2·322– 2·376	2·376– 2·430	2·430– 2·484	2·484– 2·538	2·538– 2·592	2·592– 2·646	2·646– 2·700	2·700– 2·754	Number measured.	Median length.
II	5-9-32			2 *1*	8 *3*	21 *8*	34 *13*	39 *15*	31 *12*	20 *8*	19 *7*	23 *9*	17 *6*	16 *6*	16 *6*	10 *4*	5 *2*	2 *1*				263	2·101
„	30-10-32		1 *–*	7 *3*	11 *4*	24 *10*	25 *10*	24 *10*	17 *7*	15 *6*	22 *9*	21 *9*	16 *7*	11 *4*	17 *7*	16 *7*	9 *4*	9 *4*	1 *–*			246	2·158
IV	3-9-31							1 *–*	3 *1*	5 *2*	15 *6*	22 *9*	14 *6*	32 *13*	58 *24*	52 *21*	26 *11*	12 *5*	2 *1*	1 *–*		243	2·403
„	15-9-31					1 *1*	– *–*	– *–*	– *–*	8 *7*	7 *6*	6 *5*	15 *13*	14 *12*	23 *20*	29 *25*	11 *9*	3 *3*				117	2·395
„	1-10-31							2 *2*	– *–*	– *–*	7 *6*	6 *5*	13 *12*	9 *8*	18 *16*	26 *23*	23 *20*	9 *8*				113	2·434
„	21-10-31						1 *1*	3 *3*	4 *3*	1 *1*	13 *11*	9 *8*	18 *15*	3 *3*	17 *14*	25 *21*	15 *13*	7 *6*	2 *2*			118	2·400
„	5-11-31								1 *1*	2 *2*	6 *5*	7 *6*	12 *10*	18 *15*	18 *15*	31 *26*	15 *13*	9 *8*	1 *1*			120	2·419
„	16-11-31					1 *1*	– *–*	– *–*	1 *1*	3 *3*	5 *4*	6 *5*	10 *9*	10 *9*	22 *19*	31 *27*	16 *14*	10 *9*				115	2·430
„	30-11-31							2 *1*	2 *1*	4 *3*	6 *4*	11 *8*	12 *8*	16 *11*	20 *14*	29 *20*	25 *18*	13 *9*	2 *1*			142	2·426
„	14-12-31						1 *1*	1 *1*	– *–*	2 *2*	9 *8*	4 *4*	8 *7*	9 *8*	20 *19*	22 *20*	21 *19*	10 *9*	1 *1*			108	2·431
„	29-12-31					1 *1*	3 *3*	1 *1*	5 *4*	8 *7*	10 *8*	10 *8*	6 *5*	6 *5*	14 *12*	20 *17*	21 *18*	10 *8*	5 *4*			120	2·417
„	11-1-32				1 *1*	– *–*	1 *1*	2 *2*	2 *2*	5 *5*	6 *6*	8 *7*	10 *9*	8 *7*	15 *14*	24 *22*	21 *20*	3 *3*	– *–*	1 *1*		107	2·416
„	25-1-32						1 *1*	1 *1*	6 *6*	5 *5*	4 *4*	12 *12*	4 *4*	8 *8*	13 *13*	21 *20*	17 *17*	9 *9*	– *–*	1 *1*		102	2·420
„	8-2-32				1 *1*	*–*	1 *1*	3 *2*	5 *4*	15 *12*	13 *10*	12 *10*	12 *10*	10 *8*	15 *12*	14 *11*	16 *13*	5 *4*	2 *2*			124	2·325
„	22-2-32						1 *1*	2 *2*	5 *5*	7 *7*	4 *4*	12 *12*	11 *11*	11 *11*	11 *11*	19 *18*	10 *10*	10 *10*	2 *2*			105	2·376
„	7-3-32				1 *1*	1 *1*	2 *2*	5 *4*	6 *5*	5 *4*	3 *2*	12 *10*	7 *6*	12 *10*	20 *16*	17 *14*	23 *19*	7 *6*	2 *2*			123	2·398
„	16-5-32							2 *2*	1 *1*	5 *5*	8 *8*	9 *9*	21 *20*	11 *11*	17 *16*	12 *12*	8 *8*	7 *7*	2 *2*			103	2·351
„	30-5-32				1 *1*	2 *1*	5 *3*	4 *2*	14 *8*	5 *3*	18 *11*	20 *12*	25 *15*	9 *5*	14 *8*	21 *13*	17 *10*	9 *5*	2 *1*			166	2·299
„	13-6-32		1 *–*	– *–*	– *–*	2 *–*	6 *1*	15 *4*	24 *6*	27 *6*	35 *8*	39 *9*	43 *10*	41 *10*	62 *15*	65 *15*	38 *9*	25 *6*	– *–*	1 *–*		424	2·349
„	27-6-32				5 *3*	2 *1*	2 *1*	7 *5*	13 *9*	7 *5*	11 *8*	15 *10*	19 *13*	17 *12*	27 *19*	15 *10*	6 *4*					146	2·301
„	11-7-32					5 *2*	8 *3*	11 *3*	25 *8*	29 *9*	26 *8*	30 *9*	32 *10*	62 *19*	45 *14*	23 *7*	19 *6*	2 *1*	2 *1*			319	2·312
„	25-7-32				3 *1*	3 *1*	18 *7*	6 *2*	23 *8*	24 *9*	23 *8*	26 *9*	29 *10*	32 *12*	38 *14*	29 *10*	19 *7*	3 *1*	1 *–*			277	2·292
„	8-8-32			1 *–*	2 *1*	7 *3*	11 *5*	15 *6*	25 *10*	16 *7*	14 *6*	25 *10*	20 *8*	34 *14*	36 *15*	19 *8*	8 *3*	4 *2*	2 *1*			239	2·279
„	22-8-32				1 *–*	8 *3*	8 *3*	18 *7*	19 *8*	23 *9*	21 *8*	21 *8*	30 *12*	32 *13*	29 *12*	23 *9*	12 *5*	3 *1*				248	2·277
„	5-9-32				3 *1*	8 *4*	16 *7*	14 *6*	23 *10*	22 *10*	13 *6*	22 *10*	18 *8*	30 *14*	23 *10*	16 *7*	12 *5*	1 *–*				221	2·322
„	30-10-32				2 *1*	14 *6*	14 *6*	18 *7*	19 *8*	18 *7*	21 *9*	22 *9*	28 *12*	24 *10*	28 *12*	20 *8*	9 *4*	2 *1*	1			240	2·250

Station.	Date.	1·188–1·242	1·242–1·296	1·296–1·350	1·350–1·404	1·404–1·458	1·458–1·512	1·512–1·566	1·566–1·620	1·620–1·674	1·674–1·728	1·728–1·782	1·782–1·836	1·836–1·890	1·890–1·944	1·944–1·998	1·998–2·052	2·052–2·106	Number measured.	Median length.
I	3-9-31						1 *1*	2 *2*	13 *15*	18 *20*	17 *19*	13 *15*	21 *24*	4 *4*					89	1·709
„	15-9-31		1 *3*	– *–*	– *–*	3 *9*	3 *9*	4 *11*	9 *26*	5 *14*	6 *17*	4 *11*							35	1·608
„	21-10-31			1 *3*	–	– *–*	– *–*	4 *10*	8 *21*	10 *26*	4 *10*	5 *13*	5 *13*	1 *3*					38	1·655
„	21-3-32										3 *7*	8 *18*	9 *20*	11 *25*	7 *16*	4 *9*	2 *5*		44	1·848
„	28-3-32							1 *1*	3 *2*	5 *3*	13 *8*	22 *13*	34 *21*	41 *25*	27 *16*	14 *9*	4 *2*		164	1·842
„	5-4-32						1 *1*	3 *2*	8 *5*	21 *14*	24 *16*	18 *12*	29 *20*	16 *11*	19 *13*	5 *3*	2 *1*		146	1·777
„	18-4-32					1 *1*	– *–*	4 *3*	6 *5*	13 *11*	18 *15*	20 *17*	20 *17*	27 *22*	9 *7*	3 *2*			121	1·779
„	16-5-32											8 *7*	4 *3*	9 *8*	20 *17*	32 *28*	26 *22*	17 *15*	116	1·973
„	23-5-32							1 *1*	6 *4*	14 *10*	19 *14*	23 *17*	29 *21*	21 *15*	17 *12*	6 *4*	3 *2*		119–30 m. (⅛) 139	1·795
„	„							1 *1*	2 *1*	9 *7*	12 *9*	14 *10*	25 *18*	34 *25*	22 *16*	11 *8*	6 *4*	1 *1*	30–0 m. 137	1·845
„	„							6 *1*	32 *4*	79 *10*	107 *13*	129 *16*	170 *20*	139 *17*	107 *13*	41 *5*	21 *3*	1 *–*	119–0 m. calc. 832	1·802
„	30-5-32					1 *1*	3 *3*	6 *6*	14 *13*	20 *19*	15 *14*	11 *10*	24 *22*	6 *6*	6 *6*	1 *1*	1 *1*		110–30 m. (⅛) 108	1·712
„	„				3 *3*	2 *2*	4 *4*	9 *9*	21 *20*	21 *20*	15 *15*	9 *9*	9 *9*	4 *4*	2 *2*	2 *2*	– *–*	1 *1*	30–0 m. 102	1·652
„	„				3 *–*	8 *1*	22 *3*	45 *6*	105 *14*	141 *19*	105 *14*	75 *10*	153 *20*	40 *5*	38 *5*	8 *1*	6 *1*	1 *–*	110–0 m. calc. 750	1·700
„	7-6-32						5 *2*	7 *3*	35 *17*	50 *24*	37 *18*	26 *13*	18 *9*	19 *9*	7 *3*	3 *1*			118–30 m. (⅛) 207	1·684
„	„				1 *1*	2 *2*	6 *7*	11 *13*	18 *21*	21 *24*	15 *17*	5 *6*	7 *8*	1 *1*					30–0 m. 87	1·635
„	„				1 *–*	2 *–*	31 *3*	46 *4*	193 *17*	271 *24*	200 *18*	135 *12*	97 *9*	96 *9*	35 *3*	15 *1*			118–0 m. calc. 1122	1·679
„	13-6-32					1 *2*	– *–*	8 *17*	10 *21*	9 *19*	9 *19*	3 *6*	4 *8*	2 *4*	1 *2*				47	1·650
„	27-6-32							3 *13*	5 *21*	3 *13*	3 *13*	7 *29*	1 *4*	1 *4*	1 *4*				24	1·701
„	11-7-32						2 *1*	14 *8*	19 *10*	26 *14*	32 *17*	23 *13*	28 *15*	28 *15*	10 *5*	1 *1*			183	1·726
„	25-7-32							10 *5*	30 *14*	34 *16*	51 *24*	40 *19*	30 *14*	14 *7*	2 *1*				211	1·708
„	8-8-32					1 *2*	7 *12*	15 *26*	5 *9*	10 *18*	8 *14*	5 *9*	4 *7*	2 *4*					57	1·625
„	22-8-32			1 *1*	– *–*	2 *2*	5 *4*	15 *11*	27 *20*	19 *14*	26 *20*	24 *18*	11 *8*	2 *2*					132	1·667
„	5-9-32					1 *2*	4 *10*	3 *7*	8 *20*	5 *12*	7 *17*	3 *7*	6 *15*	3 *7*	1 *2*				41	1·674
„	30-10-32					1	1	–	–	1	5	–	2	–	1				11	1·706
II	3-9-31						2 *1*	21 *6*	44 *12*	54 *14*	70 *19*	76 *20*	69 *18*	31 *8*	9 *2*	2 *1*			378	1·727
„	15-9-31			1 *1*	1 *1*	3 *3*	5 *4*	9 *8*	10 *8*	13 *11*	22 *18*	11 *9*	23 *19*	18 *15*	3 *3*				119	1·718
„	1-10-31							2 *2*	7 *7*	9 *9*	14 *14*	18 *18*	24 *23*	21 *20*	5 *5*	2 *2*			102	1·785
„	21-10-31							2 *1*	8 *6*	20 *14*	16 *11*	25 *18*	22 *16*	22 *16*	20 *14*	5 *4*	1 *1*		141	1·782
„	16-11-31								4 *11*	1 *3*	8 *21*	3 *8*	5 *13*	4 *11*	8 *21*	4 *11*	1 *3*		38	1·820

TABLE IV—(*continued*).

Station.	Date.	1·188–1·242	1·242–1·296	1·296–1·350	1·350–1·404	1·404–1·458	1·458–1·512	1·512–1·566	1·566–1·620	1·620–1·674	1·674–1·728	1·728–1·782	1·782–1·836	1·836–1·890	1·890–1·944	1·944–1·998	1·998–2·052	2·052–2·106	Number measured.	Median length.
II	30-11-31						1 *3*	1 *3*	1 *3*	– *–*	7 *22*	5 *16*	[illegible] *19*	[illegible] *9*	5 *16*	2 *6*	1 *3*		32	1·796
,,	21-3-32									1 *3*	3 *9*	4 *11*	10 *29*	11 *31*	2 *6*	4 *11*			35	1·836
,,	5-4-32								9 *9*	15 *15*	12 *12*	15 *15*	16 *16*	16 *16*	10 *10*	5 *5*	1 *1*	1 *1*	100	1·780
,,	16-5-32										1 *2*	8 *13*	15 *25*	16 *27*	12 *20*	5 *8*	2 *3*	1 *2*	60	1·858
,,	30-5-32								2 *2*	4 *5*	14 *16*	9 *10*	11 *13*	18 *20*	18 *20*	10 *11*	2 *2*		166–30 m. 88	1·850
,,	,,							8 *13*	10 *16*	14 *23*	12 *20*	8 *13*	6 *10*	2 *3*	– *–*	1 *2*			30–0 m. ($\frac{3}{10}$) 61	1·670
,,	,,							27 *9*	35 *12*	51 *17*	54 *18*	36 *12*	31 *11*	25 *9*	18 *6*	13 *4*	2 *1*		166–0 m. calc. 292	1·708
,,	13-6-32					1 *1*	6 *4*	18 *11*	23 *14*	22 *14*	32 *20*	28 *18*	16 *10*	8 *5*	3 *2*	2 *1*			159	1·691
,,	27-6-32								1 *6*	2 *12*	1 *6*	6 *37*	4 *25*	1 *6*	1 *6*				16	1·769
,,	11-7-32							2 *1*	3 *2*	4 *3*	33 *22*	36 *24*	29 *19*	27 *18*	14 *9*	2 *1*	1 *1*		151	1·779
,,	25-7-32						2 *1*	4 *3*	12 *9*	24 *17*	27 *19*	17 *12*	30 *21*	15 *11*	6 *4*	1 *1*			165–30 m. 139	1·731
,,	,,					1 *1*	3 *3*	18 *18*	23 *23*	22 *22*	16 *16*	13 *13*	4 *4*						30 -0 m. 100	1·634
,,	,,					1 *–*	5 *2*	22 *9*	35 *15*	46 *19*	43 *18*	30 *13*	34 *14*	15 *6*	6 *3*	1 *–*			165–0 m. 239	1·688
,,	8-8-32						3 *1*	4 *1*	23 *7*	44 *14*	63 *20*	86 *28*	58 *19*	22 *7*	6 *2*	– *–*	1 *–*		310	1·739
,,	22-8-32				*–*	1 *–*	6 *2*	9 *3*	22 *8*	41 *16*	51 *19*	63 *24*	43 *16*	23 *9*	3 *1*	1 *–*			264	1·729
,,	5-9-32					1 *–*	– *–*	4 *2*	18 *7*	34 *13*	40 *16*	71 *28*	56 *22*	24 *10*	5 *2*				253	1·751
,,	30-10-32							2 *10*	– *–*	1 *5*	4 *20*	6 *30*	3 *15*	3 *15*	1 *5*				20	1·760
IV	3-9-31								7 *9*	8 *10*	10 *12*	11 *13*	11 *13*	13 *16*	19 *23*	3 *4*			82	1·809
,,	15-9-31							4 *7*	5 *8*	10 *16*	7 *11*	8 *13*	6 *10*	7 *11*	7 *11*	7 *11*			61	1·762
,,	25-26-1-32						1 *2*	– *–*	4 *6*	9 *14*	11 *17*	10 *15*	9 *14*	12 *18*	7 *11*	2 *3*			65	1·771
,,	2-5-32									3 *8*	5 *14*	8 *22*	8 *22*	7 *19*	4 *11*	1 *3*			36	1·799
,,	16-5-32							3 *2*	2 *1*	14 *10*	14 *10*	36 *26*	34 *24*	25 *18*	10 *7*	2 *1*			140	1·784
,,	30-5-32								2 *4*	1 *2*	10 *20*	7 *14*	8 *16*	10 *20*	7 *14*	4 *8*	1 *2*		50	1·819
,,	13-6-32						1 *1*	1 *1*	3 *4*	5 *7*	5 *7*	13 *18*	9 *12*	12 *16*	19 *26*	4 *5*	1 *1*		73	1·836
,,	27-6-32							1 *4*	2 *8*	2 *8*	5 *20*	3 *12*	8 *32*	2 *8*	2 *8*				25	1·782
,,	11-7-32						1 *–*	6 *2*	16 *6*	28 *11*	19 *8*	30 *12*	60 *24*	57 *23*	28 *11*	7 *3*			252	1·806
,,	25-7-32					2 *1*	4 *2*	15 *7*	25 *12*	30 *15*	32 *16*	29 *14*	31 *15*	25 *12*	8 *4*	3 *2*			204	1·719
,,	8-8-32							5 *3*	25 *15*	10 *6*	20 *12*	28 *17*	29 *17*	31 *19*	19 *11*				167	1·774
,,	22-8-32					1 *–*	4 *1*	9 *3*	29 *10*	45 *16*	36 *13*	42 *15*	40 *14*	43 *15*	24 *9*	5 *2*			278	1·748
,,	5-9-32					1 *–*	1 *–*	9 *4*	37 *16*	39 *16*	48 *20*	33 *14*	23 *10*	23 *10*	16 *7*	5 *2*	2 *1*		237	1·710
,,	30-10-32							3	10	18	12	15	4	16	8				86	1·730

On the Biology of *Calanus finmarchicus*. III. Vertical Distribution and Diurnal Migration in the Clyde Sea-Area.

By

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With 4 Figures in the Text.

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INTRODUCTION.

Of recent years the attention of a number of workers has been directed towards the problem of vertical distribution of plankton organisms, and in particular to the diurnal migrations made by many of these animals.

Russell (1926) and others have considered that variation in the intensity of light throughout every 24 hours was the main cause of such changes in vertical distribution.

Despite one or two facts which, at first sight, fail to support it, this hypothesis taken as a whole seems to explain the vertical movements of the plankton and, until the full explanation is found, it may be taken as a good working hypothesis. It appears probable from the evidence that change in light intensity, while playing a large part in controlling diurnal migrations, is not the sole factor concerned.

The results of the work on Calanus up to the present may be summed up as follows. The young stages and nauplii are found in the upper layers of water ; the older stages live deeper and the males usually live deeper than the females. In the words of With (1915, p. 28), and neglecting the difference between the sexes, " the younger the stage of development the nearer the surface do the specimens live."

These general conclusions on the vertical distribution of Calanus arrived at by different workers are based on hauls taken in the open waters of the oceans and to depths down to 1500 metres. The hauls were made with closing nets hauled through distances varying from 50 to 700 metres at one step.

Most of the work on the diurnal migrations of Calanus, on the other hand, has been done by Russell in the English Channel, in water where the depth is only 50–70 metres. Hauls were taken for the most part with non-closing nets hauled horizontally through the water, the depth of fishing being recorded by a special instrument. Esterly (1911, 1912) investigated the diurnal migrations of Calanus and other copepods from hauls taken with a number of different nets and spread over a period of years. Hauls were taken from a maximum depth of 550 fathoms.

More recently Gardiner (1933) has studied the vertical distribution and diurnal migration of Calanus in the North Sea, using the improved form of the " Hardy " plankton indicator for collecting. The depth here is about 35 fathoms.

In all these cases the waters investigated are subject to considerable movement either tidal or due to currents.

The Clyde Sea-Area is peculiarly suitable for work on vertical distribution of such an animal as Calanus, owing to the presence of large bodies of water practically cut off from the rest of the sea, and subject to only small tidal movements. This has been discussed in an earlier paper (Part I, p. 83) and it has been shown that the population of Calanus within an area such as Loch Fyne may be regarded as having no communication with the population outside.

INVESTIGATIONS IN THE CLYDE SEA-AREA.

On two occasions during the year 1932 the vertical migrations of *Calanus finmarchicus* were studied over a period of 24 hours, at Station IV (Strachur) in Loch Fyne. It is a pleasure to express here my thanks to R. Kerr, Skipper, and D. Burnie, Boat-Hand, for their willing assistance on both occasions.

Hauls were taken with the same vertical closing net used for the work on seasonal distribution (Part I, p. 85). The depth which here averages 130 metres was divided into six sections, the first from the bottom to 120 metres, then every 20 metres up to 60 metres, with two hauls of 30 metres from that level to the surface.

The first occasion on which the diurnal migration was studied was on January 25th–26th, 1932. Weather conditions were perfect throughout the early part of the investigation. There was no wind and the surface of the water was glass calm until daylight, when a light north-easterly wind rose and caused a slight rippling of the surface. The sky was clear and a bright moon (full moon 23rd) shone from 7 p.m. on 25th until 7 a.m. on 26th when light clouds passed, occasionally diminishing the light of the moon. During the remainder of 26th conditions were not so good; the sky was overcast with misty clouds and the wind went round to the south-west, causing a slightly greater disturbance of the surface.

When a second investigation of the diurnal migration of Calanus was made on July 11th–12th, conditions were very similar. The sky was less clear during the night and the moon was in its first quarter (1st quarter 11th).

Hauls were made every three hours starting at 4 p.m.; the time occupied in taking the six hauls averaged about 45 minutes. Time has been reduced to G.M.T. throughout.

For convenience, in the Figures the time to the nearest hour at which each series of hauls was begun is indicated as being the time of that series. The actual time of beginning and ending will be found in Tables I and II. The series labelled 7 a.m. on January 26th was not begun until 7.30 a.m. owing to large sheets of ice on the surface of the loch which made it difficult to obtain a position where a suitable depth would be found.

The catches were preserved by the addition of sufficient formalin to make a 5% solution in sea-water, and the counting was done in the laboratory in Russell's modification of the Bogorov tray (see Part I, p. 86). Total counts were made in every case and all the copepodite stages of Calanus were counted in each haul.

In January, Stage V copepodites formed the bulk of the catches with a small percentage of Stage IV. The time was chosen, however, with a view to obtaining data on the migrations of the adults, which were appearing in the catches about this time (see Part I, Plate II).

Unfortunately at Strachur (where the work was carried out) the number of adults present was never very high, the majority of the Stage V copepodites dying without reaching the adult state. No copepodites of Stages I, II, or III were present at this time though one or two ova and nauplii appeared in the catches.

The number of each stage present varied considerably throughout the nine series of hauls. Stage IV copepodites were consistently scarce; so few were present that they are not worth recording graphically. The Stage V copepodites formed so large a bulk that diagrams of this stage might be taken to represent the total Calanus. Males considerably outnumbered females in the proportion of 13 : 2, and were sufficiently numerous throughout to give results in which some confidence can be placed. On one occasion only were there less than 100 (98 at 10 a.m. on 26th). Females on the other hand were present in comparatively low numbers.

The repetition of this work in July was intended to give a comparison between the winter and summer broods of Calanus. Unfortunately it was not until the work on seasonal distribution had been completed that it was realised that at Strachur the majority of Calanus present at that time were essentially of a brood directly comparable with those present during the winter, since by July reproduction was practically over and the autumn–winter stock was formed. This must, therefore, be regarded rather as a comparison of the diurnal migrations of comparable broods of Calanus under winter and summer conditions of environment.

In July total numbers were much lower than they had been in January and every stage was represented. Adults were comparatively scarce. So few males were found that nothing can be said about their diurnal migrations in summer ; and though the number of females was low they were more abundant than they had been during January and some, at least, of the diagrams probably represent their diurnal migrations as accurately as the methods will allow.

Diagrams have been prepared for males, females, and Stage V copepodites in January, and for females, Stages V, IV, and III, II and I copepodites in July, showing approximately the water layers occupied by each stage at 3-hourly intervals over a period of 24 hours.

These will be seen in Figures 1–4, where they have been arranged as far as possible to compare January and July conditions. The vertical distribution of the young copepodites (Stages I, II, and III) has been expressed in one series of diagrams since their distribution was essentially the same, the slight differences being shown clearly in Table II.

In preparing these figures a base line was drawn at 135 metres for the January hauls and at 130 metres for the July hauls as these were the average depths of the mouth of the net in the nine series of hauls at each of these times. The true bottom was 3 metres below these levels.

Hauls were taken from these levels to 120 metres, from 120 to 100 metres, from 100 to 80 metres, from 80 to 60 metres, from 60 to 30 metres, and from 30 metres to the surface. The number of Calanus in each section is recorded as the percentage of Calanus at the mean depth for each 20- or 30-metre section.

This method introduces a probable inaccuracy for the 30 metre to surface and bottom to 120 metre hauls and suggests, when the Calanus were more abundant in these layers, that they were mostly right at the surface or bottom. In any case it exaggerates the importance of the numbers in these layers. This effect could have been minimized in the case of the top

30-metre haul by taking an additional haul through the top 5 or 10 metres, but at the time it was thought to be unnecessary.

Gardiner (1933, p. 597) draws attention to the difference in total numbers between day and night catches and is of the opinion that the former are usually the larger, the reverse of the condition found by Russell. Results obtained in this area suggest that there is in reality little difference. There was considerable variation throughout both periods of investigation. In January the largest and smallest catches were taken during the night while daylight catches were by no means small. If the results are averaged the night catches are slightly the larger. In July the largest and smallest catches were taken during daylight and but little difference is to be observed in the average of day and night catches.

The times of astronomical sunrise and sunset at Strachur were :—

January	25th	Sunset	4.27 p.m.	G.M.T.
	26th	Sunrise	8.37 a.m.	,,
July	11th	Sunset	8.27 p.m.	,,
	12th	Sunrise	3.58 a.m.	,,

I am indebted to Captain C. H. Brown for the correct times.

RESULTS AND DISCUSSION.

Introduction.

As far as can be ascertained statements on the vertical distribution of the different stages of Calanus are based on hauls taken during the course of a cruise for the purpose of investigating plankton in general. Results obtained by this method indicate that the first and second copepodites inhabit water above 50 metres and that third copepodites live from 100 to 50 metres. The fourth copepodites are generally distributed, but are more numerous from 100 to 50 metres than from 50 metres to the surface ; and the fifth copepodites are generally distributed. Females appear to live from 100 to 50 metres and males from 300 to 50 metres. (Störmer, 1929.)

This is, of course, in general agreement with the statement of With (1915, p. 28) that the younger the stage the nearer the surface will it be found.

Bogorov (1932) found all the copepodite stages inhabiting the upper layers (25 metres) in the Barents and White Seas. (It has not been possible to determine at what time of the day or in what month of the year these results were obtained.)

Farran (1927, p. 142) records the presence of the young stages in the surface layers of the water off the south coast of Ireland.

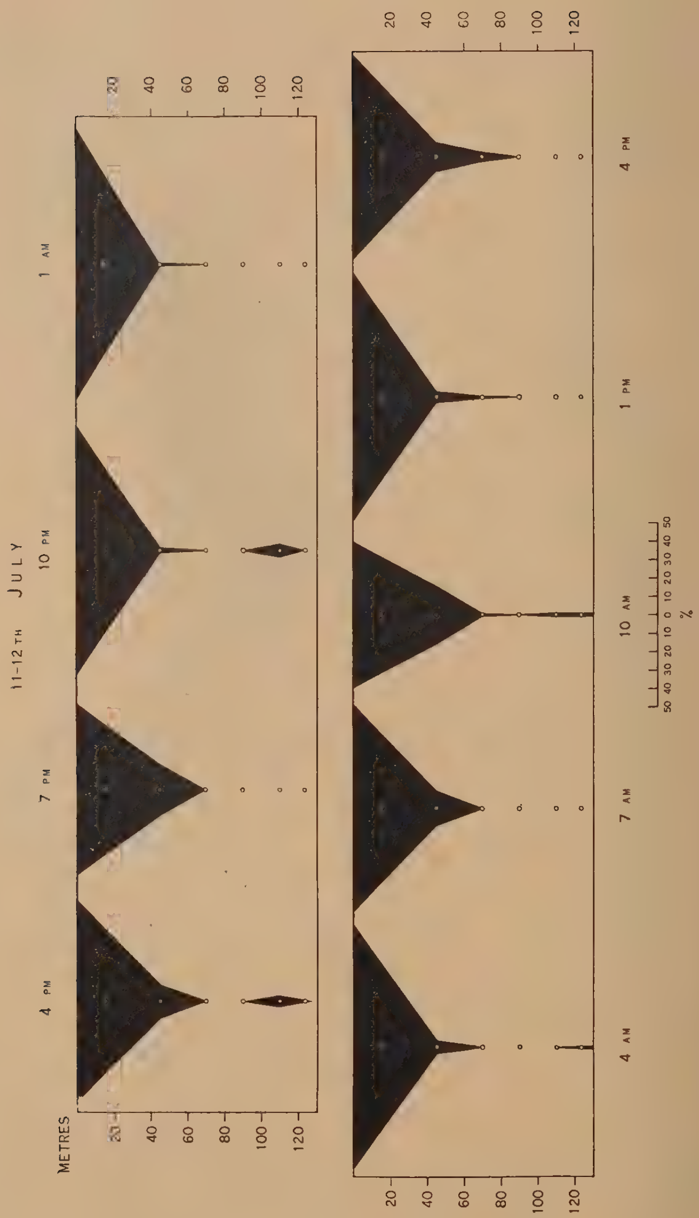

Fig. 1.—Diagram showing vertical distribution of copepodite Stages I, II, and III, at 3-hourly intervals during 24 hours on July 11th–12th. Sunset July 11th at 8.27 p.m., sunrise July 12th at 3.58 a.m.

Gran also (Paulsen, 1906) states that the young especially live at the surface in the Norwegian Sea. Gardiner (1933) using three 'Hardy' plankton indicators towed at different depths in the North Sea concluded that Calanus Stages III and IV were always to be found in the upper layers, whereas Stages V and VI lived deeper, the adults most frequently being found below the fifth copepodites.

Worthington (1931), on the other hand, working on the diurnal migration of the freshwater plankton of Lakes Lucerne and Victoria Nyanza, found (p. 432) that " in the case of nearly every species, the adults migrate less far than the young." He concludes that " the young is more susceptible to changing light intensity than the adult, or in other words, as it grows up it becomes adapted to resist intense light."

OVA AND NAUPLII.

Though the ova and nauplii present in the hauls made at Strachur on July 11th and 12th were not counted, it was observed that in every case they were most abundant in the 30-metre to surface hauls. A few were found in the 60- to 30-metre hauls, but not in sufficient numbers to indicate that they were performing a vertical migration.

During the course of the work on seasonal distribution in the Clyde Sea-Area at Stations I and II hauls were taken in two sections (from the bottom to 30 metres and from 30 metres to the surface) from March 7th until June 13th (June 7th at Station I) and again on July 25th and August 8th. The purpose of this, as explained elsewhere, was to simplify counting during the time when diatoms might be expected to be abundant.

It has, however, thrown additional light on the vertical distribution of all stages of Calanus during this time.

Reference to Tables II and III (Part I, pp. 104–107) will show that ova and nauplii were always more abundant above 30 metres than below if we neglect the occasions when the numbers were relatively small. The only exception was at Station I on May 23rd when the numbers of all nauplii and copepodites below 30 metres were greater than those above, and the ova were about equally divided. As a rule the numbers found below 30 metres were small and indicated that the centre of distribution lay above 30 metres.

YOUNG COPEPODITES (STAGES I, II, AND III).

Figure 1 shows the vertical distribution of the young copepodites at 3-hourly intervals during 24 hours beginning at 4 p.m. on July 11th. At 4 p.m. and at 7 p.m. most of the young stages were above 45 metres. The two series of hauls taken between sunset and sunrise, namely, at

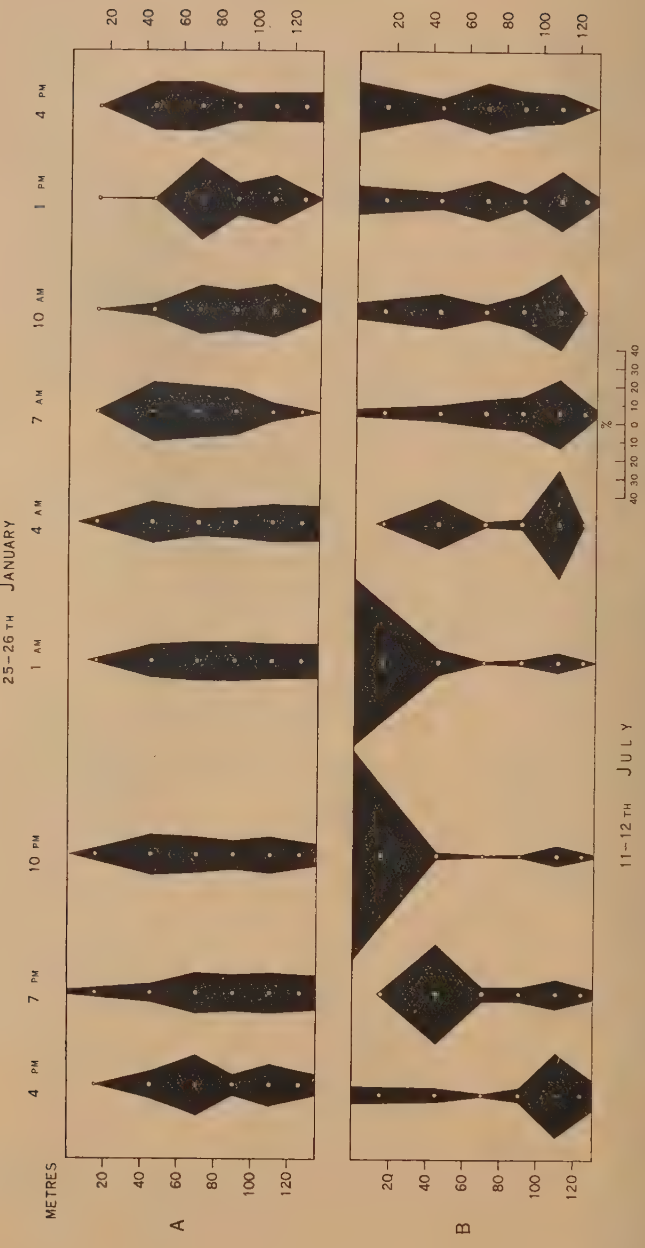

FIG. 2.—Diagram showing vertical distribution at 3-hourly intervals during 24 hours, A, of male Calanus on January 25th–26th; B, of Stage IV copepodites on July 11th–12th.

10 p.m. and 1 a.m., were very much alike and show a movement towards the surface of most of those Calanus which had been between 45 and 70 metres before sunset. The sun rose at 3.58 a.m. and the hauls taken at 4 a.m. show a tendency to return to the conditions found in daylight on the 11th. These conditions were re-established by 7 a.m. By 10 a.m. a greater proportion had left the surface layers and a very few had descended into water as deep as 90 metres. The numbers found in the 80- to 60-metre haul were, however, relatively insignificant.

The two series taken in the afternoon of 12th (1 p.m. and 4 p.m.) show an upward movement of those Calanus which had been below 45 metres at 10 a.m. On reference to the figures in Table II for the first three copepodite stages it will be seen that this slight vertical movement is practically restricted to the third copepodites. A very few of the Stage II copepodites were found below 30 metres and the first copepodites remained above 30 metres throughout.

Reference to Tables II and III in Part I (pp. 104–107), however, shows that this was not always the case at those stations situated in open water. On one occasion at Station II (May 16th), and on several occasions at Station I, a number of first copepodites was found below 30 metres. In every case where the numbers were large enough to be reliable there were many more above 30 metres than below, with the exception of the haul made on May 23rd at Station I, when the reverse was the case. Most of the evidence obtained in this region during 1932 points to the first copepodites being concentrated above 30 metres.

This in general applies also to the second copepodites which were not found below 30 metres in daylight during the investigation of July 11th–12th.

The third copepodites, on the other hand, do show a slight diurnal migration. They descended below 30 metres, a few even below 60 metres, during the day (July 11th–12th). The vertical movements of the young copepodites may be correlated with the time of day. There was an upward movement after the sun set which was maintained during the period of darkness. At 4 a.m. as the sun was rising, a slight downward movement occurred which was more marked as the sun rose in the sky. The afternoon hauls, however, do not show any close relationship to the movement of the sun. As has already been pointed out, it is the third copepodites which are chiefly responsible for changes in the diagrams for the young stages.

From Table II (Part I, p. 104) it will be seen that the third copepodites of the first breeding period (March 21st to April 18th) were more numerous above 30 metres than below, whereas those of the two later breeding periods were (with one exception) more numerous below 30 metres.

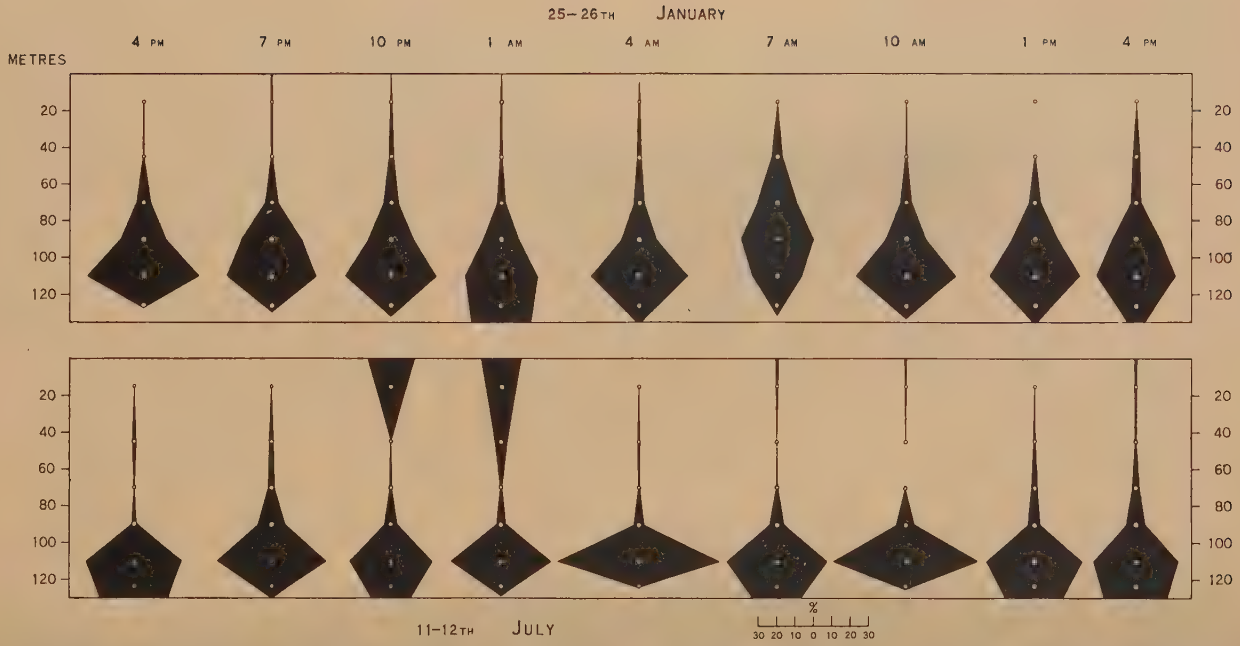

FIG. 3.—Diagram showing vertical distribution of Stage V copepodites at 3-hourly intervals during 24 hours on January 25th–26th and July 11th–12th. Sunset January 25th at 4.27 p.m., sunrise January 26th at 8.37 a.m. Sunset July 11th at 8.27 p.m., sunrise July 12th at 3.58 a.m.

Though this was so at Station I there is no indication of it at Station II. It is probable that the region usually inhabited by Stage III copepodites lies between 60 metres and the surface.

STAGE IV COPEPODITES.

Figure 2, B, shows the changes in the vertical distribution of this stage during the period from 4 p.m. on July 11th to 4 p.m. on 12th.

At 4 p.m. on 11th they were concentrated below 90 metres and were otherwise generally distributed in small numbers. Three hours later the bulk was found between 30 and 60 metres with a few in the lower levels. By 10 p.m. (sunset 8.27 p.m.) the water above 45 metres contained most of these Calanus, but, as at 7 p.m., a certain number remained in the deep water. At 1 a.m. (12th) the descent had begun though it was not very marked and most of the Calanus were still above 45 metres. The secondary maximum in the deep water was unchanged. Sunrise occurred at 3·58 a.m. and by 4 a.m. many of Stage IV were found between 30 and 60 metres, but still more had descended to the deep layer between 100 and 120 metres. By 7 a.m. only one maximum was observed and that in the deep water. The rest were distributed above this layer in diminishing numbers towards the surface. Thereafter the distribution showed little change and this stage was found at all depths.

Störmer (1929) found the fourth copepodite stage generally distributed from the bottom to the surface but more abundant between 50 and 100 metres than above that level. The deepest hauls made were from 1500 to 800 metres.

The study of the diurnal migrations of this stage made at Strachur in July suggests that they are generally distributed but tend to inhabit the deeper water and to move upwards at night to the surface layers.

There was a distinct movement towards the surface before the sun had set and by 10 p.m. they were distributed in the upper layers. By 1 a.m., however, they were leaving the surface and at 4 a.m., by which time the sun had risen, very few were found in the 30-metre to surface haul.

It is difficult to correlate the distribution found during the rest of the day with the movement of the sun. It was a bright and fairly clear day yet the general distribution showed little change from top to bottom.

The Calanus of Stage IV must be a mixture of (*a*) recently moulted third copepodites; (*b*) a proportion of those intermediate between (*a*) and (*c*) which may be regarded as true Stage IV; and (*c*) those Stage IV approaching the moult into Stage V. Since each stage can be passed in three days (see Part I, p. 92) the proportion of " transitional " Calanus may be fairly high. The vertical distribution of the third and fifth

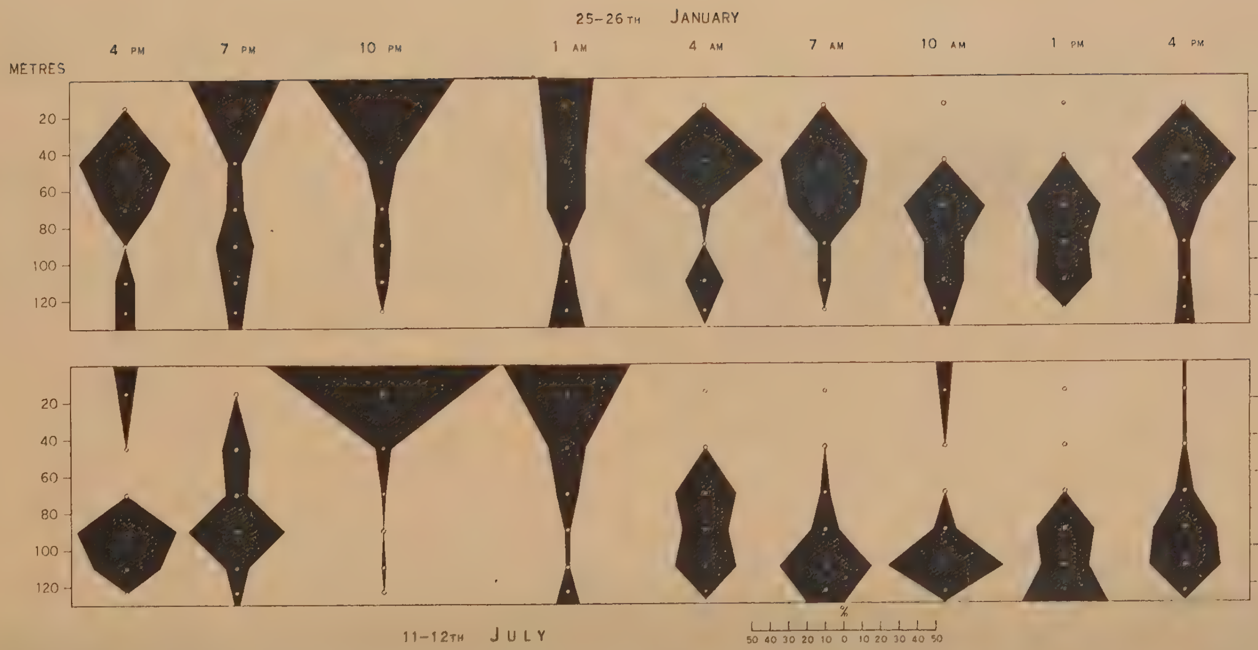

FIG. 4.- Diagram showing vertical distribution of female Calanus at 3-hourly intervals during 24 hours on January 25th–26th and July 11th–12th. Sunset January 25th at 4.27 p.m., sunrise January 26th at 8.37 a.m. Sunset July 11th at 8.27 p.m., sunrise July 12th at 3.58 a.m.

copepodites is so diametrically opposed that the distribution of those which are included under the morphological heading " Stage IV " will tend to be composite.

Physiologically, every stage will be in gradation from that immediately preceding it to the stage later. But in none will this be more apparent than in Stage IV which is transitional between those which inhabit the upper layers and those which inhabit the deep water.

It will be seen that throughout the 24 hours a certain proportion continuously inhabited that region which it seems the fifth copepodites prefer, and the numbers of such Calanus were sufficiently constant to enable the deduction to be made that these were probably soon to moult into Stage V.

Reference to Tables II and III (Part I, pp. 104–107) for Stations I and II shows more of this stage below 30 metres twice as often as above that level.

STAGE V COPEPODITES.

For this stage results were obtained in both January and July and are to be found expressed graphically in Figure 3. In January the greatest number in each series of hauls, with one exception, was found between 100 and 120 metres. Hauls taken from 100 to 80 metres contained a fair proportion but above this level Calanus was scarce. The exception occurred at 7 a.m. on 26th when the greatest number was found in the haul from 100 to 80 metres and in this series the 20-metre sections immediately above and below the 100- to 80-metre section contained about equal numbers.

The sun set at 4.27 p.m. on 25th and rose at 8.37 a.m. on 26th. A movement towards the surface in very small numbers was observed by 7 p.m. and this was maintained until 1 a.m., after which a slight descent occurred.

During the day the water above 45 metres was practically deserted by Calanus and as dusk approached a small number returned to the upper layers.

In July the majority of Stage V lived below 90 metres, and very few were found throughout the water above this level. After sunset at 8.27 p.m. a fair proportion rose to the surface layers. The descent had begun by 1 a.m., though it was not very marked. At 4 a.m., just after sunrise, the greatest concentration for this stage at any one depth was observed between 100 and 120 metres.

It is noteworthy that during January the fifth copepodites were higher in the water than during July.

The distribution of the fifth copepodite stage was remarkable and did not vary appreciably between winter and summer. They were always to be found massed in the deep water of the loch, and as a whole in January showed no movement that could be correlated with light.

In July, however, a small proportion came to the surface at night. It is suggested that those which moved up at night were the older specimens which were about to moult into adults.

Russell (1926, p. 427, and Fig. 4 ; 1928, p. 431, and Fig. 1) and Bigelow (1926, p. 202) have shown that there is a seasonal variation in the vertical distribution of Calanus.

The most striking feature shown in Figure 3 is this descent to a deeper level in July, when the sun was higher than it was in January. In the latter month the maximum angle of elevation of the sun is not much more than eleven degrees in this latitude, and much of the light incident on the surface of the water on a calm day must be reflected. In July when the sun is just past its zenith light will penetrate to a much greater depth.

The distribution as seen in Figure 3 suggests that the optimum light intensity for this stage is relatively low, since the majority are always massed together in the deep water. This is supported by the descent to a deeper level in July. Yet there is, apparently, no diurnal migration. Reference will be made to this below.

ADULTS—*Females.*

Females were found at both times in sufficient numbers to enable a comparison to be made. Figure 4 illustrates the diurnal changes in their vertical distribution in January and in July.

It will be seen that at 4 p.m. on January 25th the females were massed between 30 and 80 metres. The sun set at 4.27 p.m. and by 7 p.m. most of these females had moved into the upper 30 metres of water. Throughout the investigation a small proportion remained in the deeper water irrespective of the migration of the bulk. By 10 p.m. the accumulation in the upper layers was more marked, but by 1 a.m. the descent had begun and females were evenly distributed from the surface down to 80 metres.

At 4 a.m. they were concentrated between 30 and 60 metres with none at the surface. By 7 a.m. they were found between 30 and 80 metres. The sun rose at 8.37 a.m. and by 10 a.m. the upper layers were quite deserted ; most were found between 60 and 80 metres, but a large proportion was distributed below 80 metres. At 1 p.m. they were fairly evenly distributed below 50 metres, and 4 p.m. on 26th saw a return to the condition in which they were found at that time on 25th.

In July, generally speaking, numbers were smaller, but three large catches brought the total numbers considerably above the January total.

At 4 p.m. on 11th the females were massed between 80 and 120 metres (one specimen was found above 30 metres). By 7 p.m. they were moving towards the surface but had not yet reached it. The sun set at 8.27 p.m., and by 10 p.m. the females were congregated in the upper 40 metres. The descent had begun by 1 a.m. The sun rose at 3.58 a.m., and at 4 a.m. all were found evenly distributed below 45 metres. By 7 a.m. few remained above 90 metres. This was more marked at 10 a.m. (one specimen found above 30 metres), and by 1 p.m. distribution was fairly even below 80 metres.

The hauls taken at 4 p.m. on 12th showed a distinct upward movement on the part of a few Calanus.

Of all the different stages of Calanus none exhibits diurnal migration so well as the females in spite of the small numbers present. In January numbers varied from 9 to 39 and averaged 25, and from the diagrams it may be assumed that these numbers are sufficient to give a true indication of their migrations.

In July numbers varied from 11 to 95 and averaged 39. The effect of such low numbers as 11 and 16 can be seen when one specimen in the top 30 metres in each case produced an apparently large discrepancy (at 4 p.m. on 11th and 10 a.m. on 12th). The largest numbers, 32, 95, 60, and 86, were found at 7 p.m., 10 p.m. on 11th and 1 a.m. and 4 p.m. on 12th. Although the bottom three metres were not sampled, on only one occasion (1 p.m.) is there any suggestion that Calanus were in this unfiltered section in relative abundance.

The results of the investigations in both January and July show that females live in the deep water during the day and move towards the surface as the sun descends, arriving at the surface after sunset.

As Russell (1925, p. 793) and Esterly (1911, p. 150) have remarked they appear to leave the surface shortly after midnight. The diagrams for January 25th–26th show a general distribution at all depths at 1 a.m., followed by an accumulation at what may be taken as the optimum, which is followed down as the sun rises. This agrees with the findings of Russell (1927, p. 237).

In July the departure from the surface appears to have been delayed and yet the descent to the deeper water was accomplished by 4 a.m., by which time distribution was general below 45 metres.

This more sudden movement is probably to be correlated with the shortness of the night in July compared with January. The sun set at about half-past eight and rose about four the next morning. This gives 7½ hours of night (compared with 16 hours in January), but twilight at dusk and at dawn was of long duration. A light glow was visible on the northern horizon throughout the whole of the night and light began to increase after 2.30 a.m. (G.M.T.).

The general distribution throughout the 24 hours of both investigations agrees well with Russell's hypothetical diurnal migrations (1927, p. 237) when the differences in time of sunset and sunrise are taken into account.

A noticeable feature of the distribution of females (as with the fifth copepodites) is the greater depth to which they descend during the day in July, compared with January. It would not appear from Figure 4 that the moon, which rose after 7 p.m. on January 25th, had any decisive effect on the movements of the females towards the surface. Its light may have restricted their upward movement within the upper 30 metres, but for this there is no evidence.

Males.

Males were present in reliable numbers only in January (averaging 160 in each series of hauls). Their diurnal migration is illustrated in Figure 2, A. At 4 p.m. (25th) more were found between 60 and 80 metres than elsewhere and below this level distribution was fairly even. The sun set at 4.27 p.m. and by 7 p.m. a few were found above 30 metres, but below 60 metres their distribution was even. From 10 p.m. until 4 a.m. distribution was practically unchanged and differed only slightly from that found at 7 p.m. By 7 a.m., however, a slight downward movement from the surface was observed, accompanied by a distinct upward movement from the bottom. The sun rose at 8.37 a.m. and at 10 a.m. the descent was more marked and the majority were evenly distributed below 60 metres. By 1 p.m. a distinct massing was observed between 60 and 80 metres while still fewer were found above this level. At 4 p.m. on 26th distribution was very similar to that found at 4 p.m. on 25th.

Males appear to be much less susceptible to the influence of light than the females. Very little change took place in their distribution below 60 metres during the course of the investigation. There was a slight movement towards the surface at night and withdrawal therefrom as light increased during the day, which agrees with the results obtained by Russell (1931, b, Fig. 3). The main difference lies in the relative amounts of movement which were between 5 and 10 metres from the surface in his case whereas few were found in the top 30 metres at any time in Loch Fyne.

The more or less general distribution throughout the 24 hours, so markedly different from that of the females, is noticeable in the results from both the English Channel and Loch Fyne. Russell's material was, however, collected in June and too close a comparison is not perhaps allowable. Unfortunately the numbers present in July were so low that no reliable conclusions can be drawn as to their distribution at that time. It is probable that the slight amount of movement in the upper layers in January is to be correlated with the conditions of light at that time of year.

The remarkable feature of their distribution is the evenness below 60 metres. It suggests that the threshold of light for the males is higher than for the females, though this is not in agreement with the statements of others that males are usually found deeper than females (Paulsen, 1906, p. 16; Russell, 1928, p. 443; Störmer, 1929, p. 25).

GENERAL DISCUSSION.

The occurrence of Calanus in large quantities at the surface during the day, often under conditions of brilliant sunshine, has been recorded on several occasions in different regions.

One of the earliest records is that made by Brook (1886, p. 48) who observed Calanus in large quantities at the surface at Tarbert (in Loch Fyne) in May and June of 1885. They appear to have been obtainable with a surface net at all times, however, though in variable numbers. Later records are those of Herdman (1919, p. 115) who observed large numbers of Calanus on the surface at Tobermory in July, 1913; Willey (Russell, 1928, p. 444) who found them swarming on the surface in September; Bigelow (1926, p. 203) who found a similar occurrence in the Gulf of Maine in July and August; Marshall and Orr (1927, p. 860) who found Calanus abundant in the surface waters in May and June and sometimes in April in the Clyde Sea-Area; and Russell (1928, p. 443) who observed a greater abundance at the surface than below in July, August, and September. Gardiner's results (1933, p. 598) show more adults near the surface than below during the early part of the day; a more general distribution thereafter; and an accumulation in deeper water during the hours of darkness. This is, in fact, a reversal of the diurnal migration found elsewhere. His results were obtained in May, at which time Calanus has been found to be abundant at the surface during the day in this area also. Sömme (1933) shows Calanus abundant at the surface during April in the Lofoten area, but this appears to be a definite migration from the deeper water preparatory to spawning.

During 1932 this phenomenon was observed here only in May and June (see Part I, Tables II and III, pp. 104-107). On May 16th all stages of Calanus were more abundant above 30 metres than below at Station I, but not at Station II. At the latter station this happened on June 13th, but on that date the closing apparatus failed to work at Station I and the haul was not divided. Routine hauls in Loch Fyne were never divided since the expected diatom increase did not appear.

At Keppel, early in May, Calanus were present at the surface but not abundant.

Russell (1926, p. 422) also shows Calanus abundant at the surface in April, but correlates this with weather conditions since a week later on a bright day no such surface swarms were observed. The impression formed from such observations as have been made in the Clyde Sea-Area is that swarming at the surface is local and of a temporary nature. It would not be surprising, therefore, if different distributions were found in samples taken 6 days apart, but it may be observed that on the two later occasions in April (8th and 29th) on which catches were made Calanus were higher in the water than might be expected if light intensity alone controlled their distribution.

Observations in the Clyde Sea-Area in 1932 confirm observations made by Marshall and Orr (1927, p. 860) in earlier years. The explanation is not apparent.

It is doubtful if it is connected with spawning since that occurs at three different periods, and moreover, Stage V copepodites are found at the surface as well as adults. This is the more surprising in view of the usual vertical distribution of this stage.

Abundant food might be the cause, but for this there was no evidence in May and June.

The marked abundance of food in the upper 30 metres is possibly the reason why the nauplii and young copepodites inhabit this section. The stimulus to withdraw from bright light does not affect the nauplii, but becomes increasingly effective as development proceeds, the reverse of the condition described by Worthington (1931), so that there is a tendency for the third copepodites to move downwards during the day. Russell (1931, a, p. 394) has shown for *Sagitta elegans* that the younger stages are able to withstand higher light intensities than are the older stages. The fourth copepodites are still more affected and, as has been suggested above, these are probably intermediate, physiologically as well as morphologically, between the young copepodites and the fifth stage. The latter, as has been shown, generally remain in deep water.

It will be necessary, then, that during the winter they should find other food than diatoms and Marshall (1924) has shown that while these bulk largely in the food other organisms, notably Crustacea, Radiolaria, and other microplankton, are used extensively at certain times of the year. If the fifth copepodites depend upon such food during the winter there will be no necessity for them to seek the upper layers at any time of the year, since diatoms will probably be sufficiently numerous in the deep water during the summer and as these become scarce other organisms suitable for food will take their place.

In adults, particularly the females, negative heliotropism in Calanus is developed to its fullest extent. It follows that spawning must occur at night when the females are able to visit the surface, since ova are found largely in the upper 30 metres, and exist as such for so short a period (24 hours, Grobben, 1881).

Worthington (1931, p. 433) suggests that the reason freshwater Crustacea perform their diurnal migrations is that they have not become adapted to withstand intense light and so must descend during the day, but return as light diminishes to those layers of water wherein abound the organisms they require for food.

The idea that food is a factor which plays an important part in controlling diurnal migration seems well founded and it would appear that a balance is struck between this and light intensity. Spawning is probably a third factor and will affect adults alone.

The peculiar vertical distribution of Calanus at a certain time of the year, which varies in different regions but always lies between April and September, is possibly due to yet another factor more potent than any of those mentioned above.

Russell (1928, 1932) has suggested that differences in the vertical distribution of Calanus at different times of the year may possibly be correlated with physiological differences between broods. It seems probable that only one brood in each region so far investigated is subject to the stimulus which induces them to reverse their normal vertical distribution, though if the swarming at the surface in April shown by Russell (1926, p. 422) was due to this stimulus then, apparently, more than one brood may be affected. It appears that it is not necessarily the same brood in each region which is thus affected, but this is not yet clear.

SUMMARY.

1. Previous work on vertical distribution and diurnal migration is described.

2. The diurnal migration of Calanus was studied on two occasions in Loch Fyne (January and July, 1932).

3. Vertical hauls were taken every three hours with a closing net dividing the total depth into six sections.

4. The results for each copepodite stage of Calanus are discussed, and January and July conditions are compared where possible.

5. Ova and nauplii were observed to be most abundant in the top 30 metres.

6. Copepodite Stages I, II, and III were most abundant above 30 metres and only the third copepodites showed any tendency to descend as the light increased.

7. Stage IV showed a migration towards the surface at night, but were generally distributed during the next day.

8. It is suggested that the results for this stage are probably confused owing to its transitional nature between the young stages living at the surface and Stage V Calanus living in deep water.

9. Stage V was found always in deep water, slight diurnal changes being ascribed to the presence of such Calanus as were about to moult into adults.

10. Females showed definite diurnal migration in both January and July.

11. Males showed a general distribution and migrated in small numbers towards the surface at night and away from it during daylight.

12. Stage V copepodites and females both lived nearer the surface in January than in July, correlated with seasonal changes in the intensity of the sunlight.

13. The presence of swarms of Calanus at the surface under conditions of bright sunlight is discussed.

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TABLE I.

NUMBERS OF CALANUS, JANUARY 25TH–26TH.

4 P.M.
(4.05–4.50 p.m.)
Depth 135 m.

Depth in metres Stage		0–30	30–60	60–80	80–100	100–120	120–Bottom	Totals
VI ♂	No.	–	26	57	21	40	28	172
	%	–	15	33	12	23	16	99
VI ♀	No.	–	9	5	–	2	2	18
	%	–	50	28	–	11	11	100
V	No.	4	54	428	1291	3110	239	5126
	%	–	1	8	25	61	5	100
IV	No.	–	1	5	2	1	1	10
Totals	No.	4	90	295	1314	3153	270	5326
	%	–	2	9	25	59	5	100

7 P.M.
(7.00–7.55 p.m.)
Depth 134 m.

VI ♂	No.	14	25	57	52	57	51	256
	%	5	10	22	20	22	20	99
VI ♀	No.	14	3	4	8	6	4	39
	%	36	8	10	21	15	10	100
V	No.	77	71	476	2196	3254	598	6672
	%	1	1	7	33	49	9	100
IV	No.	5	2	2	5	1	–	15
Totals	No.	110	101	539	2261	3318	653	6982
	%	1·5	1·5	8	32	48	9	100

10 P.M.
(10.00–10.45 p.m.)
Depth 135 m.

VI ♂	No.	15	46	43	34	43	32	213
	%	7	22	20	16	20	15	100
VI ♀	No.	17	5	2	3	2	–	29
	%	59	17	7	10	7	–	100
V	No.	56	115	364	1184	2312	636	4667
	%	1	2·5	8	25	49·5	14	100
IV	No.	1	2	1	1	1	–	6
Totals	No.	89	168	410	1222	2358	668	4915
	%	2	3	8	25	48	14	100

1 A.M.
(1.00–1.50 a.m.)
Depth 138 m.

VI ♂	No.	5	33	40	39	36	36	189
	%	2·5	17·5	21	21	19	19	100
VI ♀	No.	8	6	6	1	3	5	29
	%	27·5	21	21	3·5	10	17	100
V	No.	25	41	231	1002	2017	1783	5099
	%	0·5	1	4·5	19·5	39·5	35	100
IV	No.	–	2	1	–	–	2	5
Totals	No.	38	82	278	1042	2056	1826	5322
	%	1	1·5	5	19·5	39	34	100

4 A.M.
(4.00–4.50 a.m.)
Depth 134 m.

VI ♂	No.	6	23	15	17	21	20	102
	%	6	22·5	15	16·5	20·5	19·5	100
VI ♀	No.	–	9	1	–	3	1	14
	%	–	65	7	–	21	7	100
V	No.	12	65	171	554	1568	617	2987
	%	0·5	2	5·5	19	52·5	20·5	100
IV	No.	–	1	2	1	1	1	6
Totals	No.	18	98	*189	572	1593	639	3109
	%	1	3	6	18	51	21	100

7 A.M.
(7.30–8.25 a.m.)
Depth 133 m.

VI ♂	No.	1	39	35	31	12	5	123
	%	1	32	28	25	10	4	100
VI ♀	No.	–	13	11	2	2	–	28
	%	–	47	39	7	7	–	100
V	No.	5	123	421	802	557	144	2052
	%	–	6	21	39	27	7	100
IV	No.	–	2	1	–	1	–	4
Totals	No.	6	177	468	835	572	149	2207
	%	–	8	21	38	26	7	100

10 A.M.
(10.10–11.00 a.m.)
Depth 134 m.

VI ♂	No.	–	7	25	22	28	16	98
	%	–	7	26	22	29	16	100
VI ♀	No.	–	–	4	2	2	1	9
	%	–	–	44	22	22	11	99
V	No.	7	39	261	894	2192	679	4072
	%	–	1	6	22	54	17	100
IV	No.	–	4	1	3	–	–	8
Totals	No.	7	50	291	921	2222	696	4187
	%	–	1	7	22	53	17	100

1 P.M.
(1.00–1.40 p.m.)
Depth 135 m.

VI ♂	No.	–	2	68	28	41	16	155
	%	–	1	44	18	26·5	10·5	100
VI ♀	No.	–	1	12	8	9	–	30
	%	–	3	40	27	30	–	100
V	No.	3	21	233	900	1753	680	3590
	%	–	0·5	6·5	25	49	19	100
IV	No.	–	–	1	3	4	1	9
Totals	No.	3	24	314	939	1807	697	3784
	%	–	0·5	8	25	48	18·5	100

4 P.M.
(4.00–4.40 p.m.)
Depth 135 m.

VI ♂	No.	–	34	34	19	21	21	129
	%	–	26·5	26·5	15	16	16	100
VI ♀	No.	–	17	6	2	2	3	30
	%	–	57	20	6·5	6·5	10	100
V	No.	1	132	185	851	1436	716	3321
	%	–	4	5·5	26	43	21·5	100
IV	No.	–	3	1	1	–	1	6
Totals	No.	1	186	226	873	1459	741	3486
	%	–	5	6	25	42	21	99

* *N.B.*—This figure should be increased by not more than 30% owing to a loss during sampling.

TABLE II.

Numbers of Calanus, July 11th–12th.

4 p.m.
(4.00–4.30 p.m.)
Depth 132 m.

Depth in metres Stage		0–30	30–60	60–80	80–100	100–120	120– Bottom	Totals
VI ♂	No.	–	–	–	–	–	1	1
VI ♀	No.	1	–	–	6	4	–	11
	%	9·0	–	–	54·5	36·5	–	100
V	No.	1	7	2	9	184	149	352
	%	0·3	2·0	0·6	2·5	52·3	42·3	100
IV	No.	8	7	2	7	40	23	87
	%	9·2	8·05	2·3	8·05	46·0	26·4	100
III	No.	83	29	–	–	–	2	114
II	No.	36	–	–	–	1	1	38
I	No.	7	–	–	–	–	–	7
III+II	No.	126	29	–	–	1	3	159
+I	%	79·4	18·0	–	–	0·6	2·0	100
Totals	No.	136	43	4	22	229	176	610
	%	22·3	7·0	0·7	3·6	37·5	28·9	100
7 p.m. (7.00–7.38 p.m.) Depth 125 m.								
VI ♂	No.	–	–	–	2	2	–	4
VI ♀	No.	–	5	4	17	4	2	32
	%	–	15·6	12·5	53·1	12·5	6·3	100
V	No.	–	10	15	62	250	82	419
	%	–	2·4	3·6	14·8	59·6	19·6	100
IV	No.	10	125	19	18	37	22	231
	%	4·3	54·1	8·2	7·8	16·2	9·5	100·1
III	No.	258	239	1	–	–	1	499
II	No.	243	8	–	–	–	–	251
I	No.	118	–	–	–	–	–	118
III+II	No.	619	247	1	–	–	1	868
+I	%	71·3	28·4	0·15	–	–	0·15	100
Totals	No.	629	387	39	99	293	107	1554
	%	40·5	24·9	2·5	6·4	18·8	6·9	100
10 p.m. (10.00–10.38 p.m.) Depth 130 m.								
VI ♂	No.	1	–	1	–	2	–	4
VI ♀	No.	83	8	2	–	2	–	95
	%	87·4	8·4	2·1	–	2·1	–	100
V	No.	61	2	3	24	161	105	356
	%	17·1	0·6	0·9	6·7	45·2	29·5	100
IV	No.	213	12	3	4	31	14	277
	%	76·9	4·3	1·1	1·4	11·2	5·1	100
III	No.	216	6	–	–	12	–	234
II	No.	52	2	–	–	4	–	58
I	No.	6	–	–	–	4	–	10
III+II	No.	274	8	–	–	20	–	302
+I	%	90·7	2·6	–	–	6·6	–	99·9
Totals	No.	632	30	9	28	216	119	1034
	%	61·1	2·9	0·9	2·7	20·9	11·5	100

1 A.M.
(1.00–1.45 a.m.)
Depth 129 m.

VI ♂	No.	–	–	1	–	–	–	1
VI ♀	No.	32	12	7	2	1	6	60
	%	53·3	20·0	11·7	3·3	1·7	10·0	100
V	No.	39	17	2	11	127	37	233
	%	16·7	7·3	0·9	4·7	54·5	15·9	100
IV	No.	136	30	3	7	22	9	207
	%	65·7	14·5	1·5	3·4	10·6	4·3	100
III	No.	337	6	–	1	–	1	345
II	No.	109	–	–	–	–	–	109
I	No.	18	1	1	2	–	–	22
III+II	No.	464	7	1	3	–	1	476
+I	%	97·5	1·5	0·2	0·6	–	0·2	100
Totals	No.	671	66	14	23	150	53	977
	%	68·7	6·8	1·4	2·4	15·3	5·4	100

4 A.M.
(4.00–4.45 a.m.)
Depth 131 m.

VI ♂	No.	–	2	–	–	2	–	4
VI ♀	No.	–	–	4	3	4	1	12
	%	–	–	33·3	25·0	33·3	8·3	99·9
V	No.	–	6	4	32	481	23	546
	%	–	1·1	0·7	5·9	88·1	4·2	100
IV	No.	5	39	4	9	85	3	145
	%	3·4	26·9	2·8	6·2	58·6	2·1	100
III	No.	65	16	1	1	–	3	86
II	No.	95	–	–	–	–	–	95
I	No.	42	–	–	–	–	–	42
III+II	No.	202	16	1	1	–	3	223
+I	%	90·6	7·2	0·4	0·4	–	1·3	99·9
Totals	No.	207	63	13	45	572	30	930
	%	22·3	6·8	1·4	4·8	61·5	3·2	100

7 A.M.
(7.00–7.45 a.m.)
Depth 133 m.

VI ♂	No.	1	–	–	–	–	–	1
VI ♀	No.	–	–	1	3	10	6	20
	%	–	–	5·0	15·0	50·0	30·0	100
V	No.	3	–	2	21	151	98	275
	%	1·1	–	0·7	7·6	54·9	35·6	99·9
IV	No.	5	7	12	15	30	12	81
	%	6·2	8·6	14·8	18·5	37·0	14·8	99·9
III	No.	81	64	1	–	–	–	146
II	No.	125	3	–	–	–	–	128
I	No.	84	1	–	–	–	–	85
III+II	No.	290	68	1	–	–	–	359
+I	%	80·8	19·0	0·3	–	–	–	100·1
Totals	No.	299	75	16	39	191	116	736
	%	40·6	10·2	2·2	5·3	25·9	15·8	100

10 A.M.
(10.00–10.50 a.m.)
Depth 130 m.

VI ♂	No.	–	1	–	–	–	–	1
VI ♀	No.	1	–	–	2	10	3	16
	%	6·2	–	–	12·5	62·5	18·7	99·9
V	No.	1	–	–	21	172	23	217
	%	0·5	–	–	9·7	79·2	10·6	100
IV	No.	9	14	6	14	30	–	73
	%	12·3	19·2	8·2	19·2	41·1	–	100
III	No.	74	73	3	–	1	3	154
II	No.	45	1	–	–	3	1	50
I	No.	28	–	1	–	–	–	29
III+ II	No.	147	74	4	–	4	4	233
+ I	%	63·1	31·8	1·7	–	1·7	1·7	100
Totals	No.	158	89	10	37	216	30	540
	%	29·2	16·5	1·9	6·8	40·0	5·6	100

1 P.M.
(1.00–1.40 p.m.)
Depth 129 m.

VI ♂	No.	1	–	1	–	1	–	3
VI ♀	No.	–	–	–	6	5	8	19
	%	–	–	–	31·6	26·3	42·1	100
V	No.	–	3	8	18	144	104	277
	%	–	1·1	2·9	6·5	52·0	37·5	100
IV	No.	14	10	23	9	33	14	103
	%	13·6	9·7	22·3	8·7	32·0	13·6	99·9
III	No.	145	16	3	–	–	1	165
II	No.	59	1	–	1	–	–	61
I	No.	45	–	–	–	1	–	46
III+ II	No.	249	17	3	1	1	1	272
+ I	%	91·5	6·2	1·1	0·4	0·4	0·4	100
Totals	No.	264	30	35	34	184	127	674
	%	39·2	4·5	5·2	5·0	27·3	18·8	100

4 P.M.
(4.00–4.40 p.m.)
Depth 134 m.

VI ♂	No.	–	–	1	2	1	–	4
VI ♀	No.	2	2	9	30	33	10	86
	%	2·3	2·3	10·5	34·9	38·4	11·6	100
V	No.	7	5	29	77	348	288	754
	%	0·9	0·7	3·8	10·2	46·1	38·2	99·9
IV	No.	124	61	150	105	89	28	557
	%	22·2	11·0	26·9	18·8	16·0	5·0	99·9
III	No.	495	119	36	–	–	3	653
II	No.	48	–	–	–	–	–	48
I	No.	44	–	–	–	–	–	44
III+ II	No.	587	119	36	–	–	3	745
+ I	%	78·8	16·0	4·8	–	–	0·4	100
Totals	No.	720	187	225	214	471	329	2146
	%	33·5	8·7	10·5	10·0	22·0	15·3	100

The Littoral Diatoms of the Liverpool and Port Erin Shores.

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INTRODUCTION.

CERTAIN diatoms seem to live predominantly on the foreshore. While the pelagic diatoms have received very much study, relatively little attention has been given to the shore forms. There is no satisfactory account of these organisms as they occur on the coasts of Lancashire and Isle of Man, and one may expect that they have much importance as the food of many animals. In a further paper I will deal with this question. For this reason I deal here only with those littoral diatoms found along the Mersey Beach, in the vicinity of Liverpool, and with those collected from the sandy and rocky shore of Port Erin (Isle of Man). Masses of these organisms can easily be recognised with the naked eye, discolouration of the sand and mud being due mainly to them, together with some species of desmids and dinoflagellates.

On a sandy beach like that of Port Erin, it appears as if the diatoms attain maxima of abundance during the spring and summer. They do not totally disappear from those localities during the cold months, though they become relatively scarce. During the very cold months of winter I have found diatoms on the rather muddy beach of part of the Mersey

Estuary known as the "Dingle." Apparently there are optimum conditions of sunlight and temperature for the growth and multiplication of these organisms.

General Ecology.

In their living state, littoral diatoms are seen to be attached to the coarse surface of the sand grains. A minute sand grain under the microscope seems to be a substratum for not less than 20 or 30 diatoms, of various genera and species. They may also be seen gliding between the sand grains. It is in these littoral forms that the free motion of diatoms is easily recognisable. This movement is sometimes said to be due entirely to the protoplasmic action of the part of the coleoderm in the position of the raphe. It is relatively considerable, for a minute naviculoid diatom (20μ) is able to strike an obstacle in its way, that is far larger than itself, with such force as to push it aside! A naviculoid diatom seems to move along the side of the frustule where the median line—or raphe—extends, for when this boat-like Navicula is turned on its side by just pressing delicately with a needle on the cover slip, it turns over again immediately and proceeds to move as before. The motion is more particularly noticed in those littoral diatoms which are almost free. In particular, it is in those forms that have a true conspicuous raphe, that the free motion in diatoms is best seen. In *Surirella gemma*, for example, where the raphe is less defined the motion is languid though still perceptible. The movement is a sort of backward and forward one, but it can also be a vertical or oblique one in response to the light. Phototropism is indeed marked among these forms, for on leaving the diatoms with sand in a fairly shallow enamel dish, surrounded (or even not) by a black paper, the organisms are found after a short time to be seeking the surface of the sand, so that they form, in due time, a thick yellowish green or brown layer, obviously in response to the incident light: this is the result of their motion. Most of the diatoms found on the shore exist in the free state, particularly those possessing a true raphe, but in addition, many are found connected by their valve surfaces in filaments, such as *Melosira nummuloides* and *Acnanthes longipes*, which are attached to other Algæ by more or less long stipes. Others again, such as Schizonema, are enclosed in gelatinous tubes.

Methods of Collection.

It has been suggested, as one of the best methods (8), that pieces of well-washed cotton cloth, of the size of a pocket-handkerchief, should be laid on the sand surface, when they will pick up, by their fibres, the diatoms, excluding the sand grains. This, however, proved to be of no use at all, since it was found that a great number of diatoms are left behind and are not attached to the cloth, while large amounts of small particles of sand are always picked up. Scraping the sand surface is by far the best way. The sand, with the diatoms, is placed in a fairly wide shallow glass dish, all the outside of which is covered with black paper. The sample of mud is then covered with water (taken from the shore where they were collected) to the height of, say, half an inch. This is then left for at least six hours, when practically all the diatoms form a thick yellowish green coating on the sand surface. It has been stated that the diatoms will be found floating in the layer of water above the sand surface, from which they can be pipetted or siphoned, but this is not the case, for the shore diatoms show a vigorous tendency to remain attached to the surface of sand grains and *do not* float in the water. Therefore, the best method I have found is to give the dish a slight gentle rotatory motion, when part of the diatoms float up in this water. I filter this, re-scrape the layer of diatoms from the sand surface, and filter this again through Number 16 to 20 bolting silk. This silk is sand-proof, to a sandy beach like that of Port Erin. It allows practically all the diatoms to pass through the silk as an intense yellowish green filtrate. If minute thread-like organic impurities pass through they can be easily got rid of during treatment with acids, and even these do not interfere with the diatoms mounted on a slip as do the objectionable sand grains. This silk filter even allows certain true planktonic species, thrown down by the tide from the open sea, to pass through. Thus in my filtrate such species as *Coscinodiscus radiatus*, *C. excentricus*, *Actinoptychus undulatus*, and *Biddulphia aurita*, were found. This filtration method is by far the best I have tried, and it is recommended to anyone for collecting and cleaning shore diatoms.

For studying them in the living state, the diatoms are kept in either their natural water or in Miquel solution sea-water (modified by Allen and Nelson, **1**). Before treatment with acids, for the purpose of studying the frustules, it is necessary to centrifuge them and thus get rid of the bulk of the water.

Fixing and Clearing.

Gran and Angst (**5**) state that "for the determination of the species, 95% alcohol or 4% formaldehyde in sea-water is a sufficient preservative. A solution made of 5 c.c. of 40% formaldehyde, 5 c.c. glacial acetic acid, 40 c.c. sea-water and diluted to 100 c.c. by the addition of water containing diatoms, serves for cytological studies." It is not, however, sufficient to study the diatoms when alive, though that would help in the identification of species to a certain extent, and it is necessary to see the diatom shells, depleted of their delicate organic cell-contents, so as to render the striation clear and distinct. It is always necessary to centrifuge the diatoms. They are then treated with a corrosive material. For this purpose

I have used fuming nitric acid to the extent of 1–2 c.c. to every ½ c.c. of centrifuged diatoms, and have boiled the mixture for a few seconds until the red-brown fumes of acid disappear. To this liquid distilled water is added to fill the test-tube and the mixture is cooled. A white precipitate is found in the course of an hour. The liquid is drained off and the precipitate washed repeatedly with distilled water until there is no trace of acid. The above operation takes from one to two hours, when one is left with perfect clean frustules ready for examination. The diatoms have to be mounted dry. To dehydrate the frustules, a few drops of the acid-free precipitate are taken up in a pipette and spread over a clean slide or cover slip, which is then put in an electric oven (temp. 100° C.), when all the water evaporates completely in a few minutes, and the diatom skeletons are left dry and ready for mounting.

Mounting.

The diatoms have to be mounted in a suitable medium. The visibility of markings such as the striation of diatoms is proportional to the difference between the refractive indices of the object and the medium in which it is mounted. The refractive index of the diatom silex is about 1·43, hence the diatom is not seen in concentrated sulphuric acid, as this has nearly the same refractive index. Canada balsam ($n=1{\cdot}54$), monobromide of naphthaline ($n=1{\cdot}658$), and styrax are among the media that have higher refractive indices than that of silex. I find Canada balsam and styrax unsuitable owing to their low coefficient of visibility. Monobromide of naphthaline is a liquid and is therefore unsuitable. A good mounting medium is a simple one that I have come across by mere chance and I think it is stable. A slide was found in the Liverpool Oceanography Laboratory, and on examination I found it to contain *Gyrosigma balticum*, *Pleurosigma angulatum*, and *Surirella gemma*, all mounted in a yellowish solid medium. On the slide is written " Piperine and antimony bromide," obviously indicating that this is the mounting medium. The striations of both Pleurosigma and Surirella are clear and distinct in every detail even under the ⅛-inch high-power objective. It is also very astonishing that, though the mounting was dated March 22nd, 1891, it is still as perfect as if it had been prepared to-day, despite its forty years of age, a fact which is evidence of the stability of the medium. This then must be a very good medium of high refractive index, which is not recorded in any of the references to Diatomaceæ in the Journal of the Royal Microscopical Society from 1860. I was supplied with both piperine and antimony bromide, and with the help of Dr. Daniel, I started to utilise it, with, I believe, considerable success.

Piperine is an inexpensive alkaloid of the formula $C_{17}H_{14}NO_3$. It is almost insoluble in water. It is only a very weak base and on hydrolysis gives piperidine and piperic acid. It can be obtained in a very pure state as straw-coloured crystals, with a melting point of 128° C. (262·4° F.). When it is melted it dissolves the tribromide of antimony very freely. Piperine, if heated alone directly on a bunsen flame, melts quickly into a colourless liquid which chars (blackens) with continued heat. All this may take place in the course of one minute. Bromide of antimony ($Sb\ Br_3$) melts at a lower temperature and also into a transparent liquid. Both solidify again immediately they are removed from the source of heat. In their liquid state while still hot, if they are allowed to mix, an orange or yellowish colour is produced, the intensity of the colour being dependent upon the proportion of both substances. Piperine must be used in excess of the bromide of antimony, for if the latter is in excess it crystallises out on cooling, with the result that a turbid, useless medium is formed. Different proportions of piperine and antimony bromide have been prepared and sent to the Geological Department here to find out the refractive indices. Unfortunately, I have been informed that they were unable to find these, as the medium is insoluble in their oils. It seems, however, from the examination of the various slides prepared with this mounting medium in different proportions that the best proportion is 2 parts of piperine : 1 part of $Sb\ Br_3$. Here the diatoms with their striation are so very distinct and clear that nothing more in this direction can be desired. Two parts by weight of piperine are taken with one part by weight of antimony bromide, and both are finely ground together in a mortar in their solid state, when a yellow colour immediately develops. I do not know whether this yellow material is a new chemical compound, or not. A small portion of this solid medium is put on a slide, or a cover slip, with dry diatoms. The slide or cover slip is now put on a hot plate the temperature of which must not greatly exceed 128° C. (which is the melting-point of piperine). *Under no circumstances should this medium be heated directly on the flame.* As soon as the mounting medium melts completely either lower a cover glass, or a slip, on it and take it away immediately from the source of heat, when it solidifies. A $\frac{1}{8}$-inch high-power objective gives highly satisfactory results, and the 1/12th (oil immersion) objective still better results, the striation being distinct in every detail, particularly in Pleurosigmæ which are exceedingly delicate and fine.

General Remarks.

The diatoms recorded in this paper are true littoral forms, but among them the reader will notice certain species as Coscinodiscus, Actinoptychus, Biddulphia and the like, which are true pelagic forms. The writer believes that such forms are thrown out on the shore by the rising tide, and left there. The shore seems to be an unfavourable medium for their life, for in no instance were any of these forms found alive. The littoral diatoms here recorded include those living freely on the sand or mud, as well as those found attached to Algæ, rocks, shells, and other supports. The latter diatoms are particularly the filamentous forms. It seems also that there are no specific Algæ or water plants that are most favourable for particular diatoms; some of the filamentous forms even attach themselves to other diatoms. They are found healthy, and of different species attached to red, brown, and green Algæ.

Three main spots have been examined, namely, the "Jetty" (Pier Head, Liverpool), "Dingle shore" along the Merseyside, and the sandy beach of Port Erin (Isle of Man). It is curious to find a few freshwater forms living along the shore of the River Mersey where the water is brackish, but still covered periodically by flood tides. It seems as if the diatoms of the shore can stand water of different salinities. Common forms—particularly the Nitzschiates and some filamentous forms—are found both along the brackish Merseyside and on the highly saline beach of Port Erin. It may be the light—which is important in the process of assimilation—that is the main factor controlling the abundance of shore diatoms. It may be that these organisms get their food substances from the water that covers them at high tide, but I think it probable that drainage from the land, to the shore, is the condition that matters most. So there is still much to be done by comparing other beaches, where there is very much less land drainage carrying resolved sewage constituents, with the Dingle and Port Erin Bay.

CLASSIFICATION.

The classification adopted here is based on those of West and Fritsch (1927), and Lebour (1930).

DIATOMALES or BACILLARIALES.

Centricæ

Discoidæ

Families Coscinodiscaceæ
Melosiraceæ.

Solenoidæ

Family Rhizosoleniaceæ.

Biddulphioidæ

Family Biddulphiaceæ.

PENNATÆ

Fragilarioideæ

Families	Fragilariaceæ Tabellariaceæ Meridionaceæ.

Achnanthoideæ

Family	Achnanthaceæ.

Naviculoideæ

Families	Naviculaceæ Cymbellaceæ.

Nitzschioideæ

Family	Nitzschiaceæ.

Surirelloideæ

Family	Surirellaceæ.

LIST OF SPECIES IDENTIFIED.

Group **Centricæ.**

Family *Coscinodiscaceæ.*

Genus Coscinodiscus.

1. *Coscinodiscus excentricus* Ehr. Dingle, Port Erin, rare.
2. *C. lineatus* Ehr. Dingle, rare.
3. *C. nitidus* Greg. Port Erin, rare.
4. *C. radiatus* Ehr. Dingle, Port Erin, rare.

Genus Actinoptychus.

1. *Actinoptychus undulatus* (Bailey). Dingle, Port Erin, rare.

Family *Melosiraceæ.*

Genus Melosira.

1. *Melosira sulcata* (Ehr.).
   Orthothira marina W. Sm. Dingle shore, rare.
2. *M. nummuloides* (Lyngb.). Dingle shore, Jetty, Port Erin, abundant.

Family *Rhizosoleniaceæ.*

Genus Rhizosolenia.

1. *Rhizosolenia Shrubsolii* Cleve. Dingle, very rare.

Family *Biddulphiaceæ.*

Genus Biddulphia.

1. *Biddulphia aurita* (Lyngb.). Port Erin, few.
2. *B. granulata* Roper. Dingle, rare.
3. *B. rhombus* (Ehr.). Dingle, rare.

Genus Attheya.

1. *Attheya decora* West (?). Port Erin, very scarce.

Group **Pennatæ.**

Family *Fragilariaceæ.*

Genus Fragilaria.

1. *Fragilaria oceanica* Cleve. Jetty (Pier Head), rare.
2. *F. striatula* Lyngb. Jetty, few.

Genus Synedra.

1. *Synedra affinis* Kutz. Dingle, Port Erin, abundant.
2. *S. tabulata* (Ag.). Dingle, abundant.
3. *S. suberpa* Kutz. Port Erin, abundant.
4. *S. gracilis* Kutz. Dingle, abundant.

Family *Tabellariaceæ.*

Genus Rhabdonema.

1. *Rhabdonema arcuatum* (Lyngb.). Port Erin, abundant.
2. *R. minutum* Kutz. Dingle, abundant.

Genus Grammatophora.

1. *Grammatophora marina* (Lyngb.). Port Erin, abundant.
2. *G. serpentina* W. Sm. Port Erin, abundant.
3. *G. islandica* Ehr. Port Erin, Dingle, rare.
4. *G. angulosa* Ehr. Port Erin, Dingle, common.

Family *Meridionaceæ.*

Genus Licmophora.

1. *Licmophora flabellata* Ag. Port Erin, abundant.
2. *L. juergensii* Ag. Dingle, few. Port Erin, abundant.
3. *L. gracilis* (Ehr.). Port Erin, abundant.
4. *L. dalmatica* (Kutz.). Port Erin, abundant.
5. *L. lyngbyei* (Kutz.). Port Erin, abundant.

Family *Achnanthesaceæ.*

Genus Achnanthes.

1. *Achnanthes longipes* Ag. Port Erin, abundant.
2. *A. brevipes* Ag. Dingle Shore, Port Erin, abundant.
3. *A. subsessilis* Kutz. Dingle, Port Erin, common.

Genus Cocconeis.

1. *Cocconeis placentula* Ehr. Port Erin, abundant.
2. *C. scutellum* Ehr. Dingle, Port Erin, few.
3. *C. dirputa* Greg. Port Erin, very rare.

Family *Cymbellaceæ*.

Genus Amphora.

1. *Amphora complexa* Greg. Port Erin, abundant.
2. *A. coffæiformis* (Ag.). Port Erin, abundant.
3. *A. cymbifera* Greg. Dingle, not common.
4. *A. lævis* Greg. Port Erin, common.
5. *A. pellucida* Greg. Port Erin, common.
6. *A. pusilla* Greg. Dingle, Port Erin, rare.

Family *Naviculaceæ*.

Genus Caloneis.

1. *Caloneis liber* (W. Sm.). Dingle, Port Erin, common.
2. *C. æmula* (A. Schmidt). Port Erin, few.

Genus Diploneis.

1. *Diploneis smithii* (Breb.). Port Erin, abundant.
2. *D. elliptica* (Kutz.). Port Erin, Dingle, few.
3. *D. litoralis* (Donkin). Port Erin, common.

Genus Navicula.

1. *Navicula crucigera* (W. Sm.). Dingle, abundant.
2. *N. tumida* W. Sm. Dingle, few.
3. *N. grevillei* (Ag.). Dingle, abundant.
4. *N. bottnica* Grun. Dingle, rare.
5. *N. pusilla* W. Sm. Dingle, Port Erin, common.
6. *N. punctulata* W. Sm. Dingle, common.
7. *N. lyra* Ehr. Port Erin, rare.
8. *N. humerosa* Breb. Port Erin, Dingle, very abundant.
9. *N. pygmæa* Kutz. Port Erin, fairly abundant.
10. *N. tumens* W. Sm. Dingle, abundant.
11. *N. distans* (W. Sm.). Dingle, common.

Genus Gyrosigma.

1. *Gyrosigma attenuatum* (Kutz.). Dingle, abundant.
2. *G. hippocampus* (Ehr.). Dingle, Jetty, fairly common.
3. *G. balticum* (Ehr.). Dingle, Jetty, common.
4. *G. spencerii* (Quekett). Dingle, not common.
5. *G. distortum* (W. Sm.). Dingle, abundant.
6. *G. fasciola* (Ehr.). Dingle, common.

Genus Pleurosigma.

1. *Pleurosigma obscurum* W. Sm. Port Erin, rare. Dingle, common.
2. *P. angulatum* (Quekett). Dingle, common.

3. *P. angulatum quadratum* (W. Sm.). Dingle, very abundant in summer.
4. *P. nubecula* W. Sm. Port Erin, few.

Genus Amphiprora.

1. *Amphiprora paludosa* W. Sm. Port Erin, common.
2. *A. plicata* Greg. Port Erin, few.

Genus Tropidoneis.

1. *Tropidoneis maxima* (Greg.). Port Erin, common.
2. *T. pusilla* (Greg.). Port Erin, common.

Genus Amphipleura.

1. *Amphipleura pellucida* Kutz. Jetty, rare.
2. *A. sigmoidea* W. Sm. Jetty, rare.
3. *A. rutilans* (Trent). Dingle, Port Erin, abundant.

Family *Nitzschiaceæ.*

Genus Nitzschia.

1. *Nitzschia panduriformis* Greg. Dingle, not common.
2. *N. bilobata* W. Sm. Port Erin shore, abundant.
3. *N. vivax* W. Sm. Port Erin, abundant.
4. *N. spathulata* Breb. Port Erin, common.
5. *N. angularis* W. Sm. Dingle, common.
6. *N. closterium* W. Sm. Dingle, Port Erin, common.
7. *N. reversa* W. Sm. Dingle, Port Erin, rare.
8. *N. acicularis* (Kutz.). Dingle, abundant.
9. *N. linearis* (Ag.). Jetty, Dingle, not common.
10. *N. sigma* (Kutz.). Port Erin, very rare.
11. *N. valida* Cleve & Grun. Dingle, rare.
12. *N. tænia* W. Sm. Dingle, Port Erin, common.
13. *N. parvula* W. Sm. Jetty, very rare.
14. *N. sigmoidea* W. Sm. Dingle, few.
15. *N. litoralis* Grun. Port Erin, not common.

Genus Hantzschia.

1. *Hantzschia virgata* (Roper). Port Erin, common.
2. *N. amphioxys* (Ehr.). Dingle, rare.

Family *Surirellaceæ.*

Genus Surirella.

1. *Surirella gemma* Ehr. Dingle, very abundant in summer.
2. *S. ovata* Kutz. Jetty, Dingle, rare.
3. *S. lata* W. Sm. Dingle, very rare.

LIST OF ABBREVIATIONS.

Ag. = C. A. Agardh.
Breb. = De Brebisson.
Ehr. = D. C. G. Ehrenberg.
Hass. = A. H. Hassall.
Kutz. = F. T. Kutzing.
Lyngb. = H. C. Lyngbye.
W. Sm. = W. Smith.
Thw. = G. H. K. Thwaites.
Greg. = W. Gregory.

NOTES ON SPECIES.

The species of Coscinodiscus were never found alive on the shore. *Melosira nummuloides* seems to be a true littoral form, and was always healthy, had living chloroplasts and was reproducing, while *M. sulcata* was never found alive. The species *Attheya decora* West resembles that described by Boyer, except that the figure he gives is different from the actual specimens I examined, in that two spines are directed to opposite directions and the others are nearly straight. The length of each spine is half that of the frustule. The length of the valve is 30μ in one species and 14μ in another with varying breadth. *Synedra affinis* Kutz and *Licmophora flabellata* Ag. were attached to other green Algæ and even to other diatoms, particularly those enclosed in gelatinous tubes (Schizonema). *Rhabdonema arcuatum* (Lyngb.) was scraped from molluscan shells. The Licmophora species live more or less together among other flora on the rocky shore and not on the sands. It seems that such stipitate, as well as other filamentous forms, prefer a rocky substratum, perhaps on account of its stability; the sand grains being subject to the tidal movements. Moreover, such forms find, in the vicinity of rocks, small areas of water left behind by the tide. Such small ditches of water seem to be indispensable for the life of these diatoms, unlike the free forms, such as Navicula, which can live attached to sand grains, which are only covered by tidal water twice every twenty-four hours, but which nevertheless are able to continue living under these conditions.

ACKNOWLEDGMENTS.

I am indebted to the late Professor Johnstone for his valuable aid and advice, to Dr. Daniel for his continued interest and help in this work, to Mr. J. H. Fraser for his kind assistance, and to the Mersey Docks and Harbour Board for permission to work on the beach.

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On the Marine Cladocera from the Northumbrian Plankton.

By

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Armstrong College, University of Durham.

With 36 Figures in the Text and Diagrams A, B and C.

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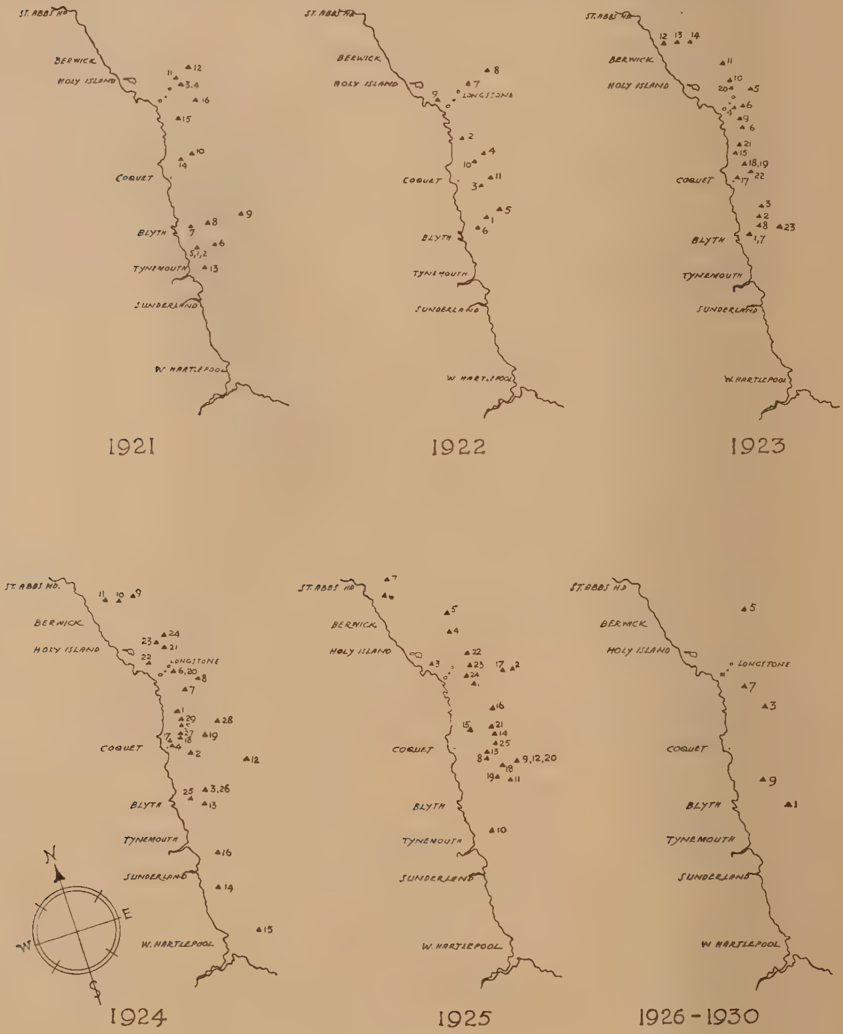
PART I. DISTRIBUTION AND SEASONAL CHANGES OF POPULATION.

INTRODUCTION.

THE material which forms the subject of this paper has been collected over a period of ten years. The samples are divisible into two groups, each including five years' catches. During the first half of the time, 1921–1925 inclusive, the stations varied from voyage to voyage but the hauls are comparable with one another as regards the nets used and the time of fishing in each case. An account of the method of sampling is given in the Dove Marine Laboratory Report for 1923, pp. 68–69 (**45**).

In 1926 a change was made in the number and kind of nets used and in the time of fishing, in order to bring the work into line with that of the Ministry of Agriculture and Fisheries. Since that year the new method has continued, and the samples have been taken each time from the same series of stations (Fig. 1). Thus, during this period the results of different years' sampling can be correlated more satisfactorily. The new method


ST. ABBS HD.
BERWICK
HOLY ISLAND
LONGSTONE
COQUET
BLYTH
TYNEMOUTH
SUNDERLAND
W. HARTLEPOOL
N
E
W
S
1921 1922 1923

1924 1925 1926-1930

Fig. 1.

of sampling is described in the Dove Marine Laboratory Report for 1926, p. 43 (**46**).

A preliminary statement as to the occurrence of the two genera of Cladocera which are found in the area sampled, during the period 1921–1923, is given in the above-mentioned Reports for 1923 and 1924 in "Plankton Investigations, No. 4 Crustacea" (**30** and **31**). In the analysis of these catches an attempt was made to indicate actual numbers of individuals, as is shown in the tables there presented. In the analyses of the subsequent years' samples only presence or absence and relative abundance is indicated, and for purposes of comparison the 1921–1923 records are here included in the same form.

Of the series of samples taken at every ten metres from surface to bottom at each station in the 1926 and subsequent catches, only three—surface, mid-water, and bottom—are here considered, in order to deal with the material on the same basis as in the earlier years when only three nets were used.

The data given in Figure 2 show the genera Evadne and Podon to be represented in the plankton. Of the former genus, only one species, *E. nordmanni*, is apparent in the samples. It is possible that a few *E. spinifera* may have been present on occasions amongst large quantities of *E. nordmanni*, but, if so, they were not distinguished. Norman and Brady include only *E. nordmanni* in their list of the Crustacea of Northumberland and Durham (**51**).

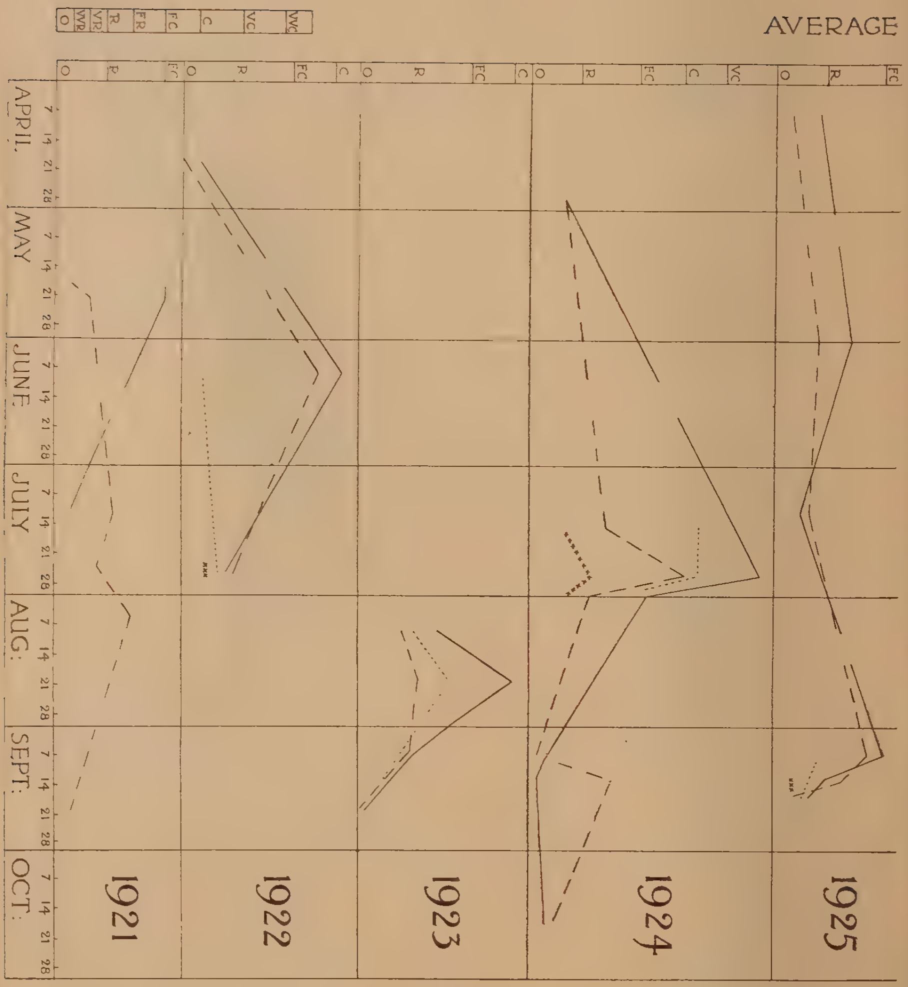
With regard to Podon, the two species, *P. polyphemoides* and *P. intermedius*, have been recorded for the district, the former being described as "not rare," and the latter as "taken occasionally." As the species are not easily identified in the course of general analyses of plankton samples, it is not proposed to discuss the distribution of the individual species of Podon in this paper. Only a general consideration of the occurrence of the two genera in the district will be undertaken. Problems of distribution and fluctuations in population will be discussed only in relation to our commonest Cladoceran, *E. nordmanni*.

ANNUAL RECORDS.

Reference to Fig. 2 and Diagrams A, B and C on pp. 186–188 will show the main facts relating to the individual years' samples as regards the occurrence of Evadne and Podon to be as indicated below.

1921.

During 1920 and 1921 abnormal conditions prevailed in the North Sea, due to a great influx of surface water from the Atlantic Ocean, as shown by the presence of *Salpa fusiformis*, *Limacina retroversa*, and other Atlantic forms in the plankton (**26**).


O
VVR
VR
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AVERAGE
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O
R
FC
C
O
R
FC
C
VC
O
R
FC
APRIL.
MAY
JUNE
JULY
AUG:
SEPT:
OCT:
7
14
21
28
1921
1922
1923
1924
1925

Fig. 2.

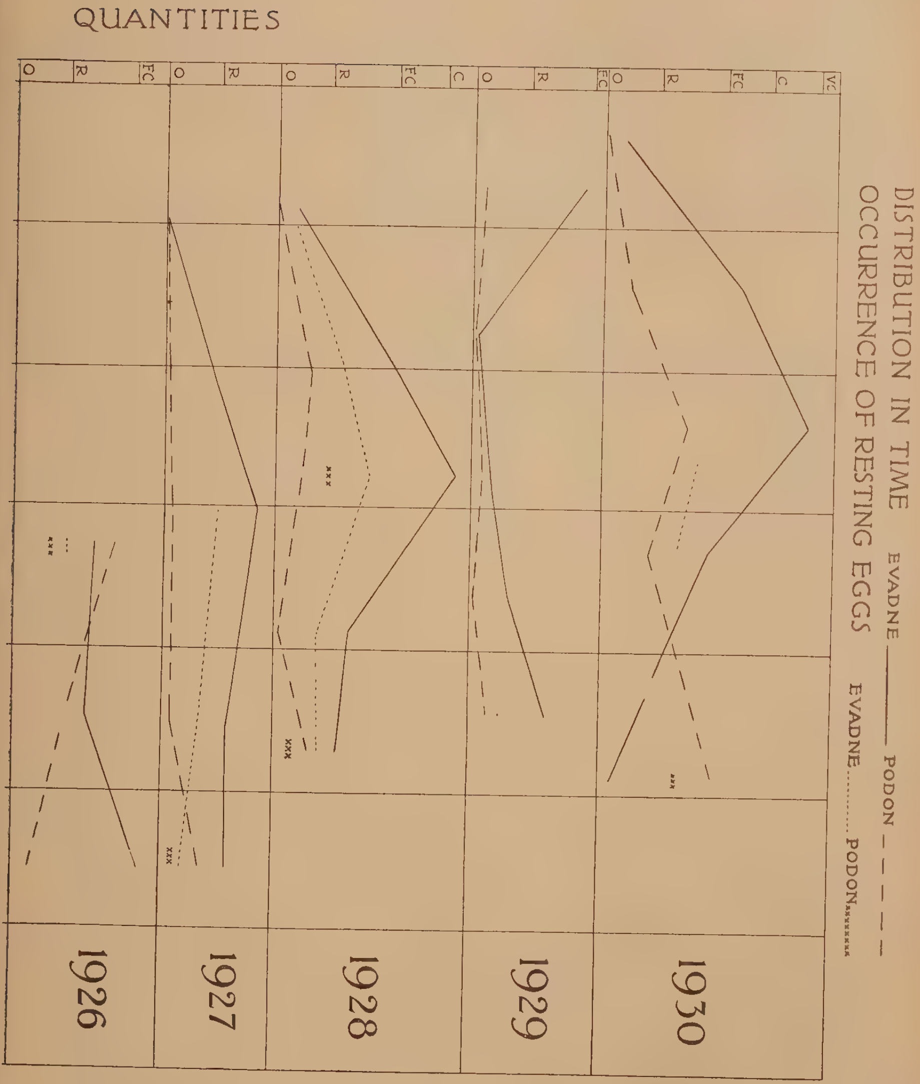

QUANTITIES
O
R
FC
C
VC
1926
1927
1928
1929
1930
DISTRIBUTION IN TIME
OCCURRENCE OF RESTING EGGS
EVADNE ——— PODON — — — —
EVADNE......... PODONxxxxxx
xxx

Fig. 2.

When the first of our series of plankton samples was taken, between May 4th and September 20th, 1921, Cladocera were present at all but two stations, namely, at 12 miles from the shore in July and inshore near Boulmer in September.

Evadne was very abundant in May at both ends of the district, after which time it was recorded only twice—in July. Podon, on the other hand, already present in May, attained a maximum early in August and persisted in decreasing numbers until the end of the sampling for that year.

No " winter eggs " or resting-eggs of either form were observed, although the catches were specially searched for them after they had been found to occur in subsequent years.

1922.

In 1922, when the Atlantic influence was abating, sampling began on April 20th when Evadne was found to be present already in the southern part of the district. Its numbers reached a maximum early in June, when it was specially abundant in the inshore region between Coquet Island and Newbiggin. On July 25th–27th, it was again taken fairly plentifully in the same region but was very sparsely represented to the north—no specimens were taken at Station 8, i.e. 7½ miles east of the Longstone.

A few resting-eggs were noted in June and rather more in July, mainly from inshore stations.

Podon appeared first in the catches in June, its numbers increasing with distance from the shore. It was present throughout the district in July, but occurred then in greatest quantity at the inshore stations. Resting-eggs were taken only once, in July (Fig. 31, p. 208).

The analysis of a series of samples taken off the Tyne on July 13th and 14th by Savage (**61**), shows that *P. leuckarti* was fairly plentiful at 11 out of 20 stations and that *E. nordmanni* was nearly three times as abundant but rather more restricted in range. Both forms were decidedly more plentiful at Station 16, i.e. 10 miles from the coast, the farthest inshore of his stations which extended to 50 miles out (Station 30). Both forms were taken also in fair quantity, even at this last station.

We have no later records for the district in this year. A single haul was made off Spurn Head in September, but no Cladocera were present.

1923.

The more normal conditions of the previous year gave place in 1923 to an exceptional flow of Arctic water into the North Sea, bringing the large variety of *Sagitta elegans* to replace *S. setosa* which had been the predominant species since 1921 (**47**).

Unfortunately, no plankton samples were undertaken before August 7th, when Evadne was present in fair numbers over the whole district. In the third week of August it was found to have become very abundant, particularly in catches from the northerly stations. In September, the only records are of small numbers at the stations near Dunstanburgh.

Developing and fully formed resting-eggs were recorded in late August and early September in much greater quantity than in the previous year—again chiefly from inshore stations.

Podon was present throughout the period, but was taken only in small numbers except in the extreme north of the district towards the end of August when it was more plentiful, especially near the shore. No resting-eggs were recorded.

1924.

Except for three hauls in the middle region of the district at the end of April, when Evadne was taken in very small numbers, no catches were made until July 13th. From that time until August 1st this form was present in abundance at all stations. Developing and fully formed resting-eggs were obtained in considerable numbers during the whole period of maximum occurrence.

Podon was present with Evadne in most of the July–August samples, but in much smaller numbers, and it was commonest inshore. During September and October it was observed in most of the catches and usually occurred in greater quantity than Evadne. Resting-eggs were recorded from three of the July–August stations, being most frequent at the end of the period.

1925.

In 1925 the first samples were taken between April 8th and 14th from ten stations covering the whole district from north to south, and extending nine miles eastward from the coast.

Evadne was present at every station and tended to be more abundant at some distance from the shore. Unfortunately, a period of six weeks elapsed before further catches were taken, when only two stations were sampled, on June 1st. Evadne was again recorded in fair numbers. In July the numbers showed a marked decline and specimens were obtained from only four of six stations. On September 7th a decided increase in abundance was noted at the more southerly stations, especially inshore, when, also, resting-eggs in an early stage of development were taken. A week later, numbers had again decreased and resting-eggs appeared only once, at Station 25.

The records for Podon show similar, but less strongly marked fluctuations, and a tendency for numbers to decrease with nearness to the coast. Podon was always the more scarce form except in July and late September. Resting-eggs were recorded only once, from Station 22.

1926.

In this year, the change in the method of sampling took place, and only three voyages were made. In July and August Evadne was taken in fair quantity throughout the district. Increased numbers reported for September were due chiefly to the catches from the most southerly stations. Resting-eggs were taken only in July, at Stations 1 and 3.

Podon was plentifully represented in July, becoming scarcer thereafter, as regards both range and numbers of individuals. Resting-eggs occurred in July at the northern station, No. 5.

1927.

Abnormal activity of the Gulf Stream, noticeable in north-eastern European waters as an increased mid-water current running through the Faroe–Shetland Channel in 1926, now produced its maximum effect, as is indicated, e.g. by the quantities of Ray's Bream taken in the North Sea from 1926 to 1928 (**77**).

Evadne, absent from all stations at the end of April, was present in small quantities throughout the district about a month later. It reached a maximum at the beginning of July, showed a slight decrease in August and was still fairly plentiful in September at the four stations fished. It is impossible, however, to give average quantities for September as the contents of three nets were lost, due to bad-weather conditions. Resting-eggs were taken in the July and subsequent samples, decreasing, in numbers and in proportion of developing to fully formed eggs, as time went on.

Podon was present from the May–June voyage onwards, but always occurred sporadically as to range, and was scarce. Resting-eggs were observed in September, at one station only.

1928.

In this year's catches Evadne appeared in April and increased in quantity up to the latter part of June, after which it decreased progressively until sampling ceased in the latter part of August. The records for resting-eggs are remarkable, in that they show these to have appeared as early as May 1st. They were taken in every month thereafter (i.e until August). The graphic representation of their distribution takes almost identically the same form as that of the average quantities of the species, over the entire period of their occurrence.

Podon made its appearance in June, touched a very low minimum in July, and increased in quantity in August. Resting-eggs were taken in both June and August.

1929.

Following upon the diminution in amount of Gulf Stream water in

1928, the North Sea again suffered an influx of surface Atlantic water in 1929, as evidenced by the occurrence of quantities of Pteropods in the plankton. The effect, however, on this occasion was less far-reaching than was the case in 1921 and 1922.

Our first samples, collected in April, showed Evadne to be already abundant in the district. After this, its numbers fell to practically nothing in May when it was present at a single offshore station only. This was followed by successive small increases in quantity from June to August. Except for a single record at Station 5 in the latter month, no resting-eggs were observed.

Podon was scarce throughout the period, with a feebly marked maximum in April. There were no resting-eggs in the samples.

1930.

Sampling began early in April of this year, and catches were made in each month until the end of August. Evadne, present sparingly in April, had reached a considerable maximum in June, after which the amounts recorded declined greatly until August when sampling ceased. Resting-eggs occurred plentifully in June, especially at offshore stations where early stages predominated, and more sparingly in July, nearer to the coast.

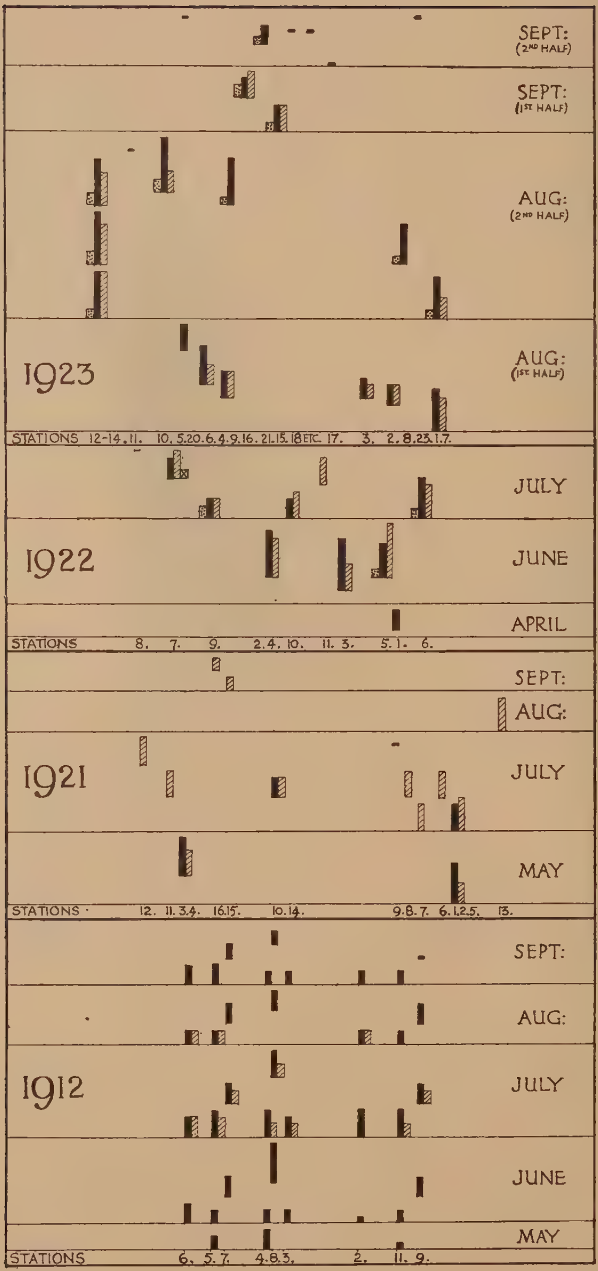
Podon appeared first in May, reached moderate numbers in June, decreased again in July, and finally rose to a marked maximum in August, when it was by far the commoner Cladoceran genus present. Stages in the development of resting-eggs were obtained from four stations on the last voyage.

Summary of Records.

Figure 2 indicates graphically the average quantities of Evadne and Podon present in all nets at all stations sampled during each voyage.

During 1921 to 1925 inclusive, these averages represent numbers of stations—and therefore also of nets—which vary considerably from time to time ; and there are, in some cases, long intervals of time between voyages. From 1926 onwards the quantities indicated are more uniform as regards the number of nets they represent, and the time intervals between voyages are more nearly equal.

As, however, series of samples taken over a fairly extensive area and generally at rather infrequent intervals can be used to acquire a general idea only as to the movements and phases of metabolic activity of planktonic forms, the two groups of data are regarded as being sufficiently comparable with one another to make it possible to use them to indicate the general trend of the fluctuations in numbers and distribution of the two genera of Cladocera under consideration, as they occur in our district.



AVERAGE QUANTITIES OF EVADNE, ▮
DO. DO. PODON, ▨

THE COLUMNS RESTING ON THE BASE LINE FOR EACH MONTHS RECORDS REPRESENT SAMPLES FROM INSHORE STATIONS. THE POSITION OF COLUMNS ABOVE THIS INDICATES RELATIVE DISTANCE OF OTHER STATIONS FROM THE COAST.

RESTING-EGGS OF EVADNE, ▦ RESTING-EGGS OF PODON, ▩

THE SIZES OF THE COLUMNS REPRESENTING NUMBERS OF RESTING-EGGS ARE COMPARABLE WITH ONE ANOTHER, BUT NOT WITH THOSE SHOWING AVERAGE QUANTITIES OF INDIVIDUALS.

LEFT AND RIGHT SIDES OF THE DIAGRAMS REPRESENT RESPECTIVELY NORTHERN AND SOUTHERN ENDS OF THE REGION.

REFERENCE TO THE MAPS WILL SHOW THE ACTUAL POSITION OF THE STATIONS INDICATED HERE BY NUMBERS (EXCEPT FOR 1912).

Diagram A.

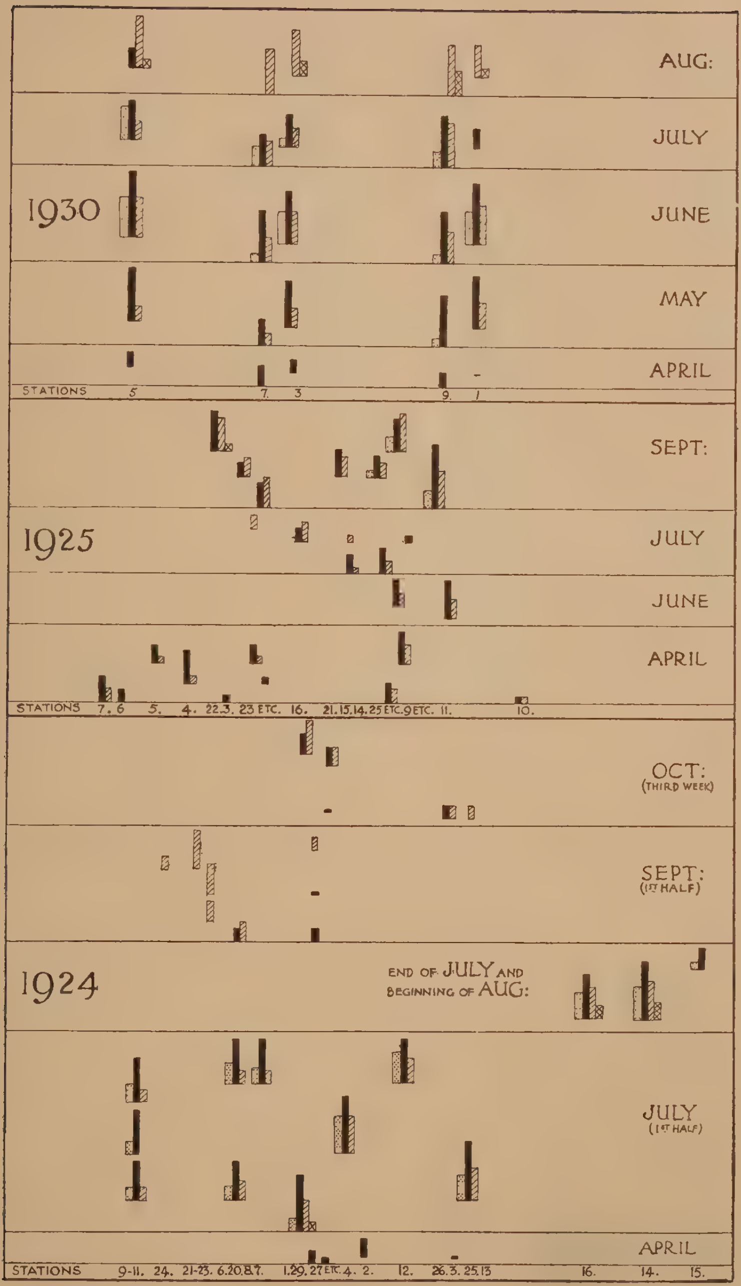
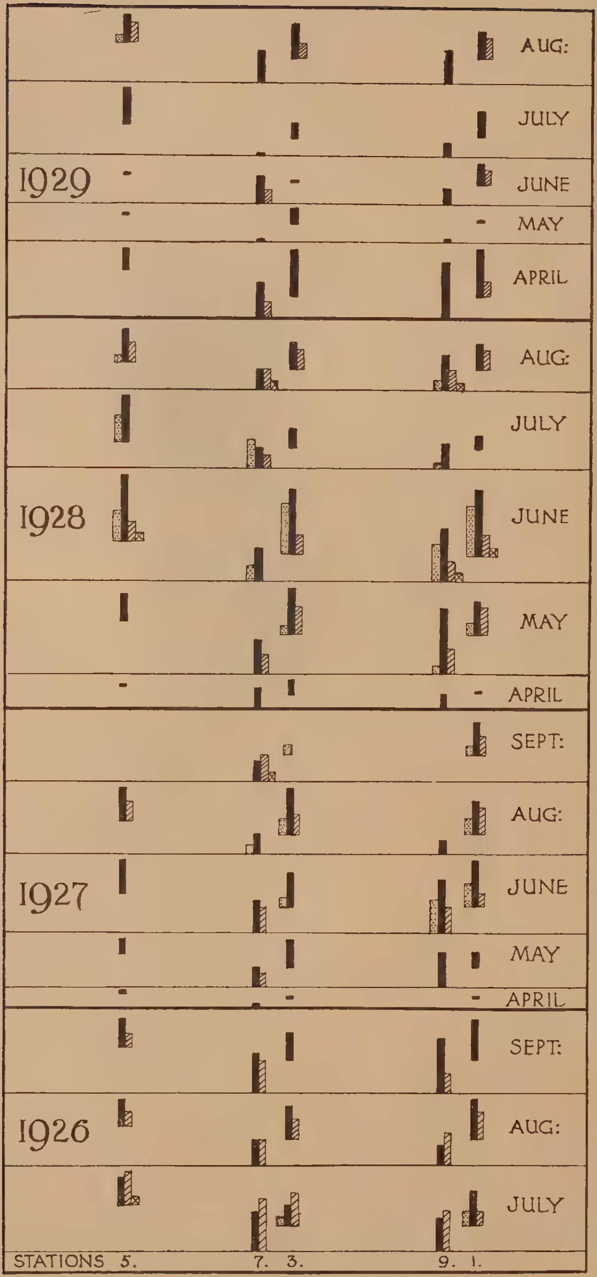

AUG:
JULY
1930
JUNE
MAY
APRIL
STATIONS 5 7. 3 9. 1
SEPT:
1925
JULY
JUNE
APRIL
STATIONS 7. 6 5. 4. 22.3. 23 ETC. 16. 21.15.14.25 ETC.9 ETC. 11. 10.
OCT: (THIRD WEEK)
SEPT: (1ST HALF)
1924
END OF JULY AND BEGINNING OF AUG:
JULY (1ST HALF)
APRIL
STATIONS 9-11. 24. 21-23. 6.20.8.7. 1.29.27 ETC. 4. 2. 12. 26.3. 25.13 16. 14. 15.

Diagram B.



AVERAGE QUANTITIES OF EVADNE, ■ | RESTING-EGGS OF EVADNE, ⊡ RESTING-EGGS OF PODON, ☒
DO. DO. PODON, ▨ | THE SIZES OF THE COLUMNS REPRESENTING NUMBERS OF
THE COLUMNS RESTING ON THE BASE LINE FOR EACH MONTHS | RESTING-EGGS ARE COMPARABLE WITH ONE ANOTHER BUT
RECORDS REPRESENT SAMPLES FROM INSHORE STATIONS. THE | NOT WITH THOSE SHOWING AVERAGE QUANTITIES OF INDIVIDUALS.
POSITION OF COLUMNS ABOVE THIS INDICATES RELATIVE DISTANCE | LEFT AND RIGHT SIDES OF THE DIAGRAMS REPRESENT RESPECTIVELY
OF OTHER STATIONS FROM THE COAST. | NORTHERN AND SOUTHERN ENDS OF THE REGION.
REFERENCE TO THE MAPS WILL SHOW THE ACTUAL POSITION OF THE STATIONS INDICATED HERE BY NUMBERS (EXCEPT FOR 1912).

Diagram C.

As the years 1921, 1923, 1927, and 1929 must be considered exceptional with regard to conditions in the North Sea, the other years' catches will be discussed first, as showing—in so far as the incompleteness of our sampling will permit—a more normal sequence of events in the life-cycles of these two genera generally, and of *Evadne nordmanni* in particular.

1. *E. nordmanni*—The "Normal" Years.

Evadne is the first Cladoceran to make its appearance in quantity near the Northumbrian coast, being present in fair numbers in April. It is by far the commoner genus on the whole, Podon, as a rule, being markedly more plentiful only from September onwards. Diagrams A—C show, as is to be expected, that Evadne is much more widely distributed throughout the area sampled under both sets of experimental conditions. The graphs indicate, furthermore, that there is a well-marked early summer maximum apparently in June (or earlier) and, for those years of which we have records, a second, but less extensive maximum in September or later is evident.

In 1924 the first maximum appears to be in July, but it must be noted that there are no records for May or June. Also, in 1925, the smallness of the first maximum, as here recorded, is probably due to the long intervals between successive samplings at this period.

It is noteworthy that the great increase in the numbers of individuals present in the samples at these times is due, not to the sudden appearance of large numbers of young, but is produced entirely, so far as our samples are concerned, by a temporary influx of adults. Although immense numbers of young forms are, no doubt, present at these times, no very small specimens are ever taken in our nets.

The population, at the times of maximal occurrence, consists principally of females with brood-pouches containing eggs and embryos in all stages of development. Males also are noted during these periods and the so-called "winter"-eggs are associated with the early maximum as well as with the later one. Indeed, our records go to show that the numbers of "winter"-eggs produced are roughly proportional to the numbers of individuals present, and that they are therefore more plentiful in summer than at the onset of winter when the physical conditions have been supposed to be most unfavourable for the continued production of parthenogenetic generations. It will be seen on reference to the graphs that the resting-eggs appear at or about the period of maximum development and continue to be observed during the subsequent decline in numbers. These findings require a consideration of the factors involved in the change from parthenogenetic to sexual reproduction. This will be dealt with later (Part II).

Occasional observations of resting-eggs as early as June have been recorded, e.g. by Hansen (**25**), and are looked upon as being unusual. Apstein, however, notes a marked occurrence of these in June on the Dutch coast and at Kiel (**2** and **3**). For our region the only record looked upon as being exceptionally early is that of both developing and fully formed resting-eggs at three stations on May 1st, 1928. Apstein gives a similar early record for Station 4 (100 miles E. of Hartlepool) in May, 1908 (**2**).

It would appear that the explanation of the frequency of resting-eggs in early summer, which is brought to light by these investigations, is to be sought in the comparative nearness of the stations to the coast, and the large number of samples taken in a restricted area, as compared with the stations used by the International Council and other investigators.

The appearance of resting-eggs in quantity at stations comparatively near the coast, such as ours are, is associated with movements of the population of *E. nordmanni* as a whole.

It is impossible to use the 1921–1925 samples to indicate movements within the district, as stations sampled on different voyages cannot be compared with one another satisfactorily ; but, from 1926 onwards, the three years 1926, 1928, and 1930 do give some suggestion of " transnatant " movements.

In 1926 the population, represented over the whole area, was rather more abundant inshore in July, i.e. at the end of the first sexual period as indicated by the presence of a few resting-eggs. Diagram C shows a slight offshore movement in August, while in September there is evidence of a return to the inshore stations which was coincident with the onset of the decidedly early autumn maximum.

After April, 1928, in which month the small numbers present occurred mainly inshore, resting-eggs were being produced in all the months for which we have records, and the population was spread widely over the district.

The records for 1930 show a similar sequence of events up to the end of the summer sexual period, which ended in July, and the August records show the population to have disappeared from the district almost entirely.

It is suggested, therefore, that *E. nordmanni* seeks shallower coastal waters during the actively growing period when parthenogenetic broods are being produced ; that it remains in these regions until pairing has taken place and resting-eggs have been formed, and that it subsequently makes a migration or transnatation into deeper water. This is probably extensive after the autumn maximum and comparatively slight between the summer and autumn maxima—a difference associated with the length of time between these and with changes in physical conditions at different seasons of the year.

2. *E. nordmanni*—The "Exceptional" Years.

It is now necessary to consider the effect of the influence of surface Atlantic water in the North Sea in 1921 and again in 1929. In both years the changed conditions had the effect of speeding up the spring maximum, which occurred in April, 1929, and in May, if not earlier, in 1921. After this the numbers of Evadne decreased rapidly, the population evidently being swept away from our inshore waters.

The fact that no resting-eggs were associated with the first maximum in either year is regarded as significant, and will be discussed in relation to the general distribution of the species.

In 1921 there was no return of the population in autumn, but in 1929 numbers rose steadily from June onwards to produce an autumn maximum as is indicated by the taking of a few resting-eggs on the last voyage.

It is difficult to say what was the effect of the increased amount of Gulf Stream water in the North Sea in 1927, as the records show only one maximum, in early July, and this is capable of two interpretations. There is nothing to indicate whether it represents a much delayed early summer maximum or a greatly accelerated autumn one. The records are sufficient, nevertheless, to show that conditions were abnormal.

As the short sampling season in 1923—the year in which the influence of Arctic water was strongly marked—gives us records for August and September only, it is again impossible to do more than speculate as to its general effect on the species. From the fact that there was a distinct maximum in August, it would seem reasonable to assume that the autumn maximum had been produced unusually early. The phytoplankton of our samples has not yet been analysed, but when this is done it may be expected to throw some light on the problem.

One other point of interest, in this connection, remains to be mentioned, i.e. the occasional appearance of small numbers of individuals distinctly larger than the typical form. These were noticed first from the surface-net of Station 9 in 1925, and again on several occasions in the May–June records for 1927. A few occurred also at the beginning of July of that year. They were not noted again until 1930, when they appeared in both May and June. In the three years they were taken chiefly in the surface and mid-water nets.

These forms were remarkable also for the unusually large number of embryos contained in their brood pouches. The smallest number noted was 7, the majority had 9–11, and a few were observed with as many as 12 or 13. In May–June, and July, 1927, some were seen to be carrying resting-eggs.

Occurrence of Large Form of E. nordmanni.

Year.	Date.	Stat.	Net.	Record.
1925	April 14	9	S	9 or 10 embryos in brood pouch.
1926				
1927	May 30–June 1	1	S	early stages ; some with resting-eggs.
		3	B	,, ,, ,, ,, ,,
		5	S	,, ,, ,, ,, ,,
		7	S	,, ,, ,, ,, ,,
		9	S	9–11 embryos in brood pouch.
		,,	M	10 embryos in brood pouch.
		,,	B	early stages.
	June 30–July 3	1	S	,, ,,
		9	S	,, ,, some with resting-eggs.
1928				
1929				
1930	May 13	1	S	quite common.
		5	S	many ; one with 13 embryos.
		,,	M	11 and 12 embryos in brood pouch.
		9	M	scarce.
		,,	B	,,
	June 10	3	S	one specimen seen.
		,,	M	,, ,, ,,
		,,	B	,, ,, ,,
		5	S	several
		,,	M	one specimen seen, 7 embryos in brood pouch.

So far as 1927 and 1930 are concerned, the presence of the large form of *E. nordmanni* might possibly be considered to be associated with the influx of Atlantic water into the North Sea. The 1925 record, however, cannot be similarly explained and much remains to be discovered about the distribution of this form before it is possible to explain its presence in our coastal waters.

The only reference it has been possible to discover relating to marked variations in body-size of marine Cladocera, is that of Rammner who mentions de Lint's records for *P. polyphemoides* in the Zuider Zee where specimens taken from water of low salinity measured 500μ as against Lilljeborg's measurements of forms from more saline waters (600μ–660μ).

In relation to *E. nordmanni*, Rammner states only that individuals are bigger and have broader brood pouches at the beginning of the year than those produced towards the end of summer. If he means this as the rule rather than the exception he cannot have been referring to very large forms such as have been mentioned above. Also, if it is to be supposed that these larger, broader females are the direct products of the sexually formed resting-eggs, they ought to have been noticed in autumn also.

According to Lilljeborg, differences in shape correspond to local variations in populations, North Sea forms being ovoid or elliptical-oval and rounded posteriorly whilst the Baltic variety has a narrower body, due to the brood pouch being narrower and more pointed. He adds, furthermore, that the usual number of embryos produced by North Sea forms is 7 or 8, whereas the Baltic ones have only 3 to 5.

Our investigations show that it is necessary to have records covering a considerable period and to be sure that the forms compared occur in similar stages of the life-cycle before general statements such as the above can be made with safety.

The Northumberland population of *E. nordmanni* includes both of Lilljeborg's varieties (**35**), the proportions in which they are represented depending on the phase of activity of the species at the time. In so far as Rammner (**58**) may be understood to mean that rather larger, broader females occur at the beginning of the period of rapid increase in numbers by the production of successive parthenogenetic broods, his observations are in accord with ours. The proportion of these forms diminishes as the asexual stage of the life-cycle proceeds, until, at the time when developing resting-eggs first make their appearance in the samples, the population consists to a great extent of less bulky, more triangular forms.* These produce from 1 to 6 embryos, the majority having 2, 3, or 4. This change in body-bulk and shape, and the reduction in reproductive activity are regarded as indicating a depression in metabolic activity which is synchronous with the onset of the sexual phase. The relation of these observations to the life-cycle of marine Cladocera generally, will be considered separately below.

In this connection it may be mentioned also that the very few previous records of twin resting-eggs (Lilljeborg) have been considerably increased by these investigations. Whereas Lilljeborg observed them only in September, there are in our samples ten records for June and July as against a single one for September, indicating that not only as regards numbers of individuals present and of resting-eggs produced, but in reproductive power also, the early summer maximum is to be regarded as the chief period of activity in the annual cycle of *E. nordmanni*.

OCCURRENCE OF TWIN RESTING-EGGS.

Year.	Date.	Stat.	Net.	Record.
1924	July 13	5	S	One specimen seen.
		8	S	A few.
		9	S	,,
1925	Sept. 7	20	M	One specimen seen.
1926	July 8	1	S	A few.
1927				
1928	June 1	3	S	One specimen seen.
		9	B	,, ,, ,,
	June 24	1	S	,, ,, ,,
		1	M	A few.
		3	S	One specimen seen.
1929				
1930	June 9	1	B	,, ,, ,,

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* Sharpe (**72**) states that the brood sac may contain from 3 to 8 embryos, this causing its outline to be quite variable.

3. PODON—OCCURRENCE FROM 1921 TO 1930.

Until the species (or varieties) of Podon present at various times in the samples have been identified, it is impossible to make definite statements as to the precise activities of members of the genus, but one or two general facts may be mentioned.

As already noted, Podon makes its appearance in our district later than Evadne and is comparatively rare during the early summer. Nevertheless, it shows a maximum, generally feebly marked and more or less coincident with that of Evadne. This is followed by a decrease in numbers which, however, soon gives way to a considerable increase in population producing an autumn maximum which may involve the presence of vastly greater numbers.

It has been noted from time to time that, while individuals of Podon are indistinguishable from one another in the earlier part of the year, there is evidence of the presence of two distinct species (or varieties) in the later months. Resting-eggs were never taken in quantity, but the graphs (Fig. 2) indicate that they may appear in association with both periods of greatest population. The two maxima appear to be little affected by abnormal conditions, except for a general speeding up of activity in relation to time in 1921.

The above-mentioned data indicate that, in addition to being generally a less abundant North Sea genus than Evadne, it is also less strongly attracted to shallow coastal waters as a breeding place.

PREVIOUS RECORDS OF CLADOCERA FROM NORTHERN EUROPEAN SEAS.

1. *Northumberland.*

The only previous records of Cladocera for the Northumbrian coast are from surface and, to a less extent, bottom tow-nettings taken at long intervals in various parts of the district, between 1889 (**44**) and 1912 (**76**). Only the last of these series of samples is sufficiently complete to be comparable with the present records, and these are included in Diagram A. The distribution of the two genera in time and space may be seen to take what is regarded as the normal course. Evadne arrived from the north of the district in May, spread along the coast in June and July—being more abundant inshore in the latter month, when maximum numbers were present. It was scarce, particularly inshore, in August, and in September showed a slight tendency to return to the coast, especially towards the north. There is a decided similarity between these and the 1924 records.

Podon (identified as *P. polyphemoides*) did not make its appearance so early as Evadne. It was recorded for July and August and showed a maximum coincident with that of Evadne.

In 1899 it is evident that large numbers of both forms were present in June. The remaining records are too vague to be of value in this connection.

2. *Firth of Forth.*

T. Scott's records (**65**) for this region give no details and show only that *E. nordmanni* is more abundant than *P.* (*?*) *polyphemoides* and has a wider distribution.

3. *Clyde Sea Area.*

Marshall's records (**42**) for *E. nordmanni*, " Common in May and June, fairly common till September and frequent in October," again indicate the occurrence of two periods of maximal occurrence near the coast.

4. *English Channel.*

A consideration of Bygrave's records (**9**) of Cladocera in 1905 and 1906 shows some interesting features. He, however, made no attempt at an analysis, merely noting occurrences and making a general statement to the effect that these forms are more frequent in the western than the eastern part of the Channel, that they always appear in spring and form an important part of the plankton in summer, disappearing again in autumn, " when they form their winter-eggs and thus are able to survive the winter." (This from a record of samples taken during a period of exceptional activity of the North Atlantic Drift: Salps were present in the North Sea in 1905 and Pteropods plentiful in 1906.)

The lightship records from the western and eastern ends of the Channel (Sevenstones and Varne) show Evadne to be the commoner form in the west in 1906, while only Podon occurred at the eastern end. In 1905 Evadne was scarce to the west also.

Quarterly records from other stations (E1 and E17—10 to 20 miles offshore on the northern side) in 1906 show Evadne to be present in February, fairly common in May and abundant in August. The Plymouth records for 1906 also indicate maxima in May–June and in August–September, the latter being the greater.

Bygrave connects the general scarcity of Evadne in 1905 with a patch of water of high salinity at the western end of the Channel (near Station E1).

It is evident from the summary of records given below, that the Cladoceran population enters the Channel with the Atlantic current and normally begins to breed as soon as it reaches coastal waters. In 1905 it was evidently swept away from its usual local centre of distribution, and the fact that in 1906 the early maximum was relatively small indicates that there had not then been a complete return to normal conditions. The taking of resting-eggs only in the late summer of 1906 further accentuates the similarity between these records and ours for later years in which similar conditions prevailed in the North Sea.

SUMMARY OF BYGRAVE'S RECORDS OF EVADNE.

Year.	Month.	Stations arranged in order from W. to E.			
		Sevenstones.	E1–E17.	Plymouth.	Varne.
1905	Jan.–June	None	–	–	None.
	July	Rare	–	–	,,
	Aug.	,,	–	–	,,
	Sept.	Very rare	–	–	,,
	Oct.–Dec.	None	–	–	,,
1906	Jan.	,,	–	None	,,
	Feb.	,,	Very rare	,,	,,
	March	,,	–	Very rare	,,
	April	Rare	–	Rare	,,
	May	Rare to f. common	Common	F. rare	,,
	June	Rare to f. common	–	Rare to f. common	,,
	July	Common to rare	–	F. rare	,,
	Aug.	F. common to rare*	Common	Common	,,
	Sept.	Common	–	F. common to rare	,,
	Oct.	F. common	–	None	,,
	Nov.–Dec.	None	None	,,	,,

– indicates no samples taken. * indicates resting-eggs taken.

5. *The Irish Sea.*

The summaries of records of Cladocera given in the annual plankton reports of the Lancashire Sea-Fisheries Laboratory from 1907 to 1919 show them to refer to two species only, *Podon intermedius* and *Evadne nordmanni*. Considered together, they show the latter species to appear in the district in March or April, to increase in numbers to May or June and thereafter to fall off until September when a second maximum occurs. None are recorded later than October.

In the years 1908, 1913 and 1914, Evadne did not appear until April and, in the last two years, was always scarcer than usual. In 1912 it was not taken later than August.

Podon is shown to have a time range very similar to that of Evadne except that it generally appears rather later and persists longer.

The records are too scanty to show clearly variations in time of appearance and abundance of population from year to year, and indeed the reports frequently lay stress (perhaps rather more than would seem to be warranted) on the great constancy of occurrence of these forms.

A. Scott's records (**64**) of Cladocera from the spawning ponds at Port Erin in 1922 and 1923 indicate the presence of abnormal conditions in the earlier year, as also do our records for Northumberland. In 1923 Evadne first occurred at Port Erin in April and continued to be taken until September, while in the previous year it did not make its first appearance until June and disappeared again in August. Podon was present in 1923 from April till December excepting only August. In 1922 its range was restricted to May–July.

Gough's records (**21**) of samples taken at four lightships on the south and east coasts of Ireland in 1904 are insufficient to form a satisfactory picture of the general distribution of Cladocera in St. George's Channel and the Irish Sea although they serve to show that the population in these waters is distributed by the current entering from the south, and there is some indication of two periods of maximal abundance in inshore waters.

The fact that no Cladocera were taken at the South Arklow Lightship and their extreme scarcity at Skulmartin suggest that in this region there occurs a phenomenon similar to that noted by Bygrave and Apstein regarding the distribution of Cladocera at the eastern end of the English Channel and in the southern part of the North Sea. Apstein remarked that Cladocera were scarce in these regions, "although the physical conditions were suitable," and failed to account for this.

This matter will be discussed separately below.

6. *North Sea, Baltic Sea, etc.*

Plankton samples taken by several investigators and expeditions show *E. nordmanni* to be the commonest Cladoceran in the North Sea, on the western shores of Great Britain, in Danish waters, and in the Baltic. It is noted as being present in varying degrees of abundance at different stations, almost throughout the entire year, but always rare during the winter months. It has been mentioned as having been taken along the Norwegian coast up to 72 deg. N. lat., and, in the Atlantic, 13 deg. West of Scotland. Also, there are isolated records of its occurrence in the Barents Sea near the Murman coast and in the Irminger Current up to the south coast of Iceland.

Apstein regards the species as being abundant throughout the seas of North-West Europe during all the summer months. This conclusion is evidently based on the fact that the times of maximal abundance vary slightly from place to place and from year to year, and that the many different stations sampled were far from being equally distant from the shore. Although he quotes Hansen's records of resting-eggs taken in Dutch coastal waters in June, he does not appear to attach any significance to their production at so early a period.

Rammner, summing up records of the distribution of *E. nordmanni*, refers to its abundance in the North Sea and the Baltic and to its occurrence farther afield, but regards the Baltic as its real home. Apstein, on the other hand, considers the northern part of the North Sea to be its centre of distribution.

Rammner remarks also on its great variation in numbers from place to place, due to causes other than seasonal ones, and points out the necessity for more systematic sampling before it is possible to make a definite statement as to its distribution in a large area (such as the North Sea). He considers that currents are responsible for its distribution and notes its tendency to inhabit inshore waters.

With reference to his statement that *E. nordmanni* is not found within a distance of 100 or 200 metres from the shore, it may be noted incidentally that specimens were taken in August, 1922, in the Estuary of the River Coquet. Also, the species has been recorded by T. Scott (**67**) as being abundant at the head of Loch Fyne.

Lohmann's quantitative analyses of organisms taken in a measured volume of water, show the occurrence of two maxima in the numbers of *E. nordmanni* obtained, i.e. in June and August (1884) with a minimum between these, in July.

Investigators have remarked on apparent peculiarities in the distribution of the species, and, assuming it to be truly neritic, have had to account for its occurrence in certain places by its being carried by currents away from its normal area of distribution in coastal waters.

Rammner emphasises the effect of currents on its distribution and thinks that there may be some reason for considering the species to be a deep-sea form. Steuer goes farther and thinks that it is ridiculous not to regard *E. nordmanni* as an oceanic species since it has been shown to occur in the open ocean.

Ostenfeld explains the presence of occasional specimens along the Norwegian coast and in the Barents Sea as being due to the Gulf Stream carrying them away from the coast (of the western side of Scotland, presumably). He is unable, however, to explain the occurrence of *E. nordmanni* in the Irminger Current.

Apstein, referring to the distribution of this species, does not analyse his data, but his statements relating to that of *E. spinifera* are interesting. He regards isolated specimens taken near the Faroes as having been brought there through the influence of the Atlantic Drift. Also, while making no special reference to the exceptional conditions prevailing in 1905, he thinks that examples found in the English Channel in November, 1904, and in the south-west corner of the North Sea in the following May, might well have originated in the Atlantic Ocean. He mentions, furthermore, that the only specimens taken in any year near the Belgian Coast were obtained in May, 1905.

As 1905 is comparable with 1921, and to a less extent with 1929 as regards the cause of unusual conditions in the North Sea, the foregoing statements are of importance as emphasising the influence of an increased influx of Atlantic drift water into our coastal regions. The effect of such is evidently to interfere with the normal distribution and breeding times of the Cladoceran population, and to introduce other forms, e.g. *E. spinifera*. Its effect in 1921 and 1929 was to sweep away *E. nordmanni* from the Northumbrian coast after an early maximum in May, and to prevent the development of resting-eggs there at these times. Also, the records for 1929 show no indication of depression as regards body-shape and numbers of embryos formed, during the early part of the year. (The 1921 samples need re-examination for verification of this point.) It would thus appear that the increased amount of Atlantic drift water present produced a change in the physical conditions which are responsible, at least indirectly, for this effect. Bygrave's records for the English Channel show similar results to have been brought about there in 1905, as also do Lohmann's for the relative proportions of Podon and Evadne present at Kiel during the same period.*

From a consideration of the above data it is suggested that normally *E. nordmanni* is capable of migrating across current during the course of its denatant drift along the coast, so that it is brought into inshore waters where the environment is at first suitable for the rapid production of successive parthenogenetic broods, but which later has the effect of slowing down activity and bringing the asexual period to an end. An unusually strongly running body of water or one differently constituted from the normal coastal current may interfere very markedly with this series of events.

GEOGRAPHICAL DISTRIBUTION OF *E. NORDMANNI*.

In addition to the distribution of the species in the regions already discussed, *E. nordmanni* is also known to inhabit the Labrador Current (Hansen) and to be common off the coasts of Nova Scotia (Wright, **89**) and Massachusetts (Sharpe, **72**).

The importance of the part played by current systems as indicated above needs further consideration, and it is suggested that it is necessary to take a wider view of the geographical distribution of the species than has been done previously.

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* That similar conditions supervened in 1896 is shown by T. Scott's records for the Faroe-Shetland Channel in July and August of that year. Salps and Arachnactis larvæ were present, indicating an abnormal flow of Atlantic water. While *Podon intermedius* (or *polyphemoides*) was taken in 14 out of 19 catches, *E. nordmanni* was present in only 6 and was always rare.

It is evident from the position of the stations from which *E. nordmanni* has been observed that one cannot regard it as a neritic species except in the sense that it " prefers " coastal waters as a breeding-place. That such regions are absolutely necessary for the purpose remains to be proved.

Ostenfeld, assuming that the species was indigenous to the coasts of North-Eastern Europe, was at a loss to explain its presence near Iceland, in the open Atlantic and in the Labrador Current.

If, however, these regions of occurrence are considered in relation to Wright's and Sharpe's records for the east coast of North America, its presence can be explained. *E. nordmanni* occurring in quantity off the coasts of Massachusetts and Nova Scotia must be picked up by the Gulf Stream and carried across the Atlantic to be distributed to the English Channel and the Bay of Biscay (**75**) on the one hand, and to the west coast of Scotland, northern North Sea, Danish waters, and Baltic Sea on the other hand. Furthermore, it may be carried likewise along the Norwegian coast even so far as the Barents Sea when conditions are favourable. Since the Irminger Current branches off from the Atlantic Drift farther to the west, this assumption provides the only explanation of the occurrence of *E. nordmanni* along its course. Since it is present in the Labrador Current also, it may be said to occur in every part of the North Atlantic circulation. Thus, the species may be regarded as having two main centres of distribution, the one on the west coast of North America, the other in the coastal waters of North-Eastern Europe. That it is a regular inhabitant of the North Atlantic Ocean is evident, though to what extent it breeds under other than coastal conditions is as yet unknown.

Records of the species from the Bay of Biscay, the Mediterranean, the coast of California, and various places along the west coast of Africa indicate that it has other centres of distribution, but the records are too scattered to make it possible to discuss this point.

SCARCITY OF *E. NORDMANNI* IN CERTAIN COASTAL AREAS.

A consideration of the horizontal distribution of Cladocera in the Irish Sea, North Sea, and English Channel in relation to the Admiralty chart (Fig. 3) showing the general drift of surface water in these regions, reveals the fact that the main spread of the population is along the course of the principal coastal surface currents in the regions concerned.

In the North Sea, Cladocera have been recorded as being generally scarce to the southward of a line drawn between the Tyne (55 deg. N. lat.) and Texel (53 deg. N. lat.), that is beyond the region in which the southerly flowing coastal current crosses over from the English to the Freisian coast. That a fraction of the population is retained in the offshoots of the current which continue south to about the region of Orford Ness is shown from the analysis of Savage's samples. In these the numbers of Cladocera decrease with distance southward as far as Lowestoft, the most southerly station fished.

Distribution in the Irish Sea is explainable along similar lines. The main population enters via the south coast of Ireland in the current which passes through St. George's Channel and, on reaching the Irish Sea, is deflected with it to the east, as seen from the Liverpool and Port Erin records. That it scarcely enters the region to the west of this, in which only temporary drifts approach the Irish coast, is indicated by the lightship records of that region (South Arklow and Skulmartin). Thus, in both the above cases, major movements of population depend on the circulation of the main surface currents, and only relatively small numbers are present in those parts not directly under the influence of these.

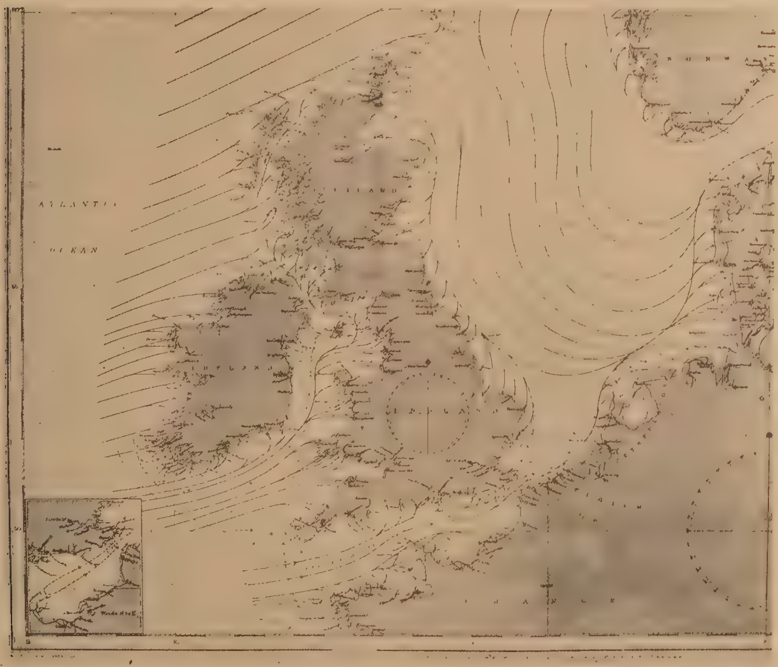


FIG. 3.—Admiralty Chart, showing direction of surface currents around the British Isles.

In the case of the English Channel, the scarcity of Cladocera in the eastern region is more difficult to account for. In consideration of the fact that the main current in which Cladocera are abundant at the western end of the Channel normally passes through the Dover Strait, would lead one to assume their presence in quantity both in the eastern part of the Channel and in the south-western region of the North Sea. Their general scarcity in these waters is probably to be accounted for in part by the effect on the current of the narrowing of the Channel eastwards, and partly to temporary conditions to be referred to shortly. On both sides of the main Channel current there are coastwise offshoots whose general tendency is to be deflected backwards. (Tidal movements here also tend in the same direction.)

If it is generally true that agamic reproduction is favoured by inshore conditions, the greater part of the Cladoceran population should be found in these parts—as it is, so far as our incomplete records including only the northern shore are able to show.

The Admiralty chart (Fig. 3) referred to includes an inset showing the temporary effect of northerly to easterly winds on the current of the Dover Strait. This illustrates that, in these circumstances, the direction of the current on the English side may be reversed and travel in the direction of C. Barfleur as far as about 1 deg. W. long. Also, the direction of the tidal streams on either side of the Dover Strait during the ebb will act in conjunction with this in its effect of further mitigating against the passage of quantities of Cladocera into this part of the Channel and through the Dover Strait into the southern North Sea. That an abnormally strong influx of surface Atlantic water into the North Sea may also accentuate this condition at times, is suggested by the entire absence of Cladocera from the Varne Lightship Station throughout the years 1905 and 1906.

Records of quantities of Cladocera in Dutch coastal waters on certain occasions—other than off the northern part of the Freisian coast—can however be accounted for only on the assumption that at times large numbers *are* able to pass through the Dover Strait, or that the temporary currents indicated as traversing the region between Lowestoft and the Hook, take part in their distribution, or that both may be contributory factors.

THE VERTICAL DISTRIBUTION OF *EVADNE NORDMANNI*.

The only material as yet available for the study of the vertical distribution of *E. nordmanni* in Northumbrian coastal waters is that taken in 1928, when all the samples were examined, i.e. the catches from the whole series of nets used at ten-fathom intervals at all stations.

The relative numbers of Evadne taken at the different depths are indicated in Fig. 4. F. S. Russell's (**59**) method of representation has been used. The narrow black lines indicate depth where no specimens were obtained.

Except in April and in a few of the later catches, when Evadne was scarce, it is shown to be present at all depths fished, i.e. down to 60 fathoms at the offshore stations with a decided tendency to be most abundant in the first 10 to 20 fathoms below the surface. If, as stated by Russell, light intensity is the main deciding factor of the depth at which a species normally lives, then the optimum intensity for *E. nordmanni* is evidently very high. Not only was it found abundantly near the surface during the summer months at times when visibility was comparatively poor, as in the early June and the August voyages, but its general distribution suffered no appreciable change when visibility was good in the later June cruise and exceptionally good in July. (A special note in the yacht's log has reference to the unusually clear conditions prevailing on July 24th to 27th.) See Table I, page 204.

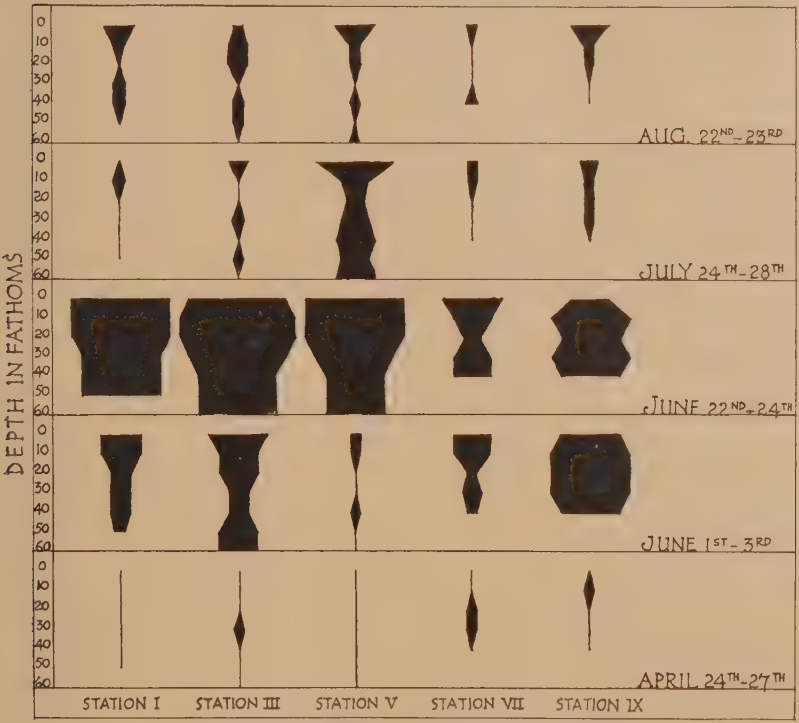


FIG. 4.—Vertical distribution of *E. nordmanni*, 1928.

Our records, therefore, bear out the general statements of other workers as to *E. nordmanni* being essentially an epiplanktonic form. Rammner however states that the species is not found actually at the surface except in dead calm weather, as it makes its way to deeper layers of water at the first sign of roughness of the sea. This does not hold good so far as our records are concerned, for the samples taken on the August voyage show a distinct aggregation of individuals at and near the surface on an occasion when the sea was moderating after a rough period. Sampling was to have begun on August 21st, but the sea was too rough for the work to be undertaken until the following day. The weather conditions prevailing during the several cruises, as recorded in the ship's log, are summarised in Table I.

The records of Stebbing and Fowler (**75**) of Cladocera in the Biscayan plankton further stress the fact of *E. nordmanni* being essentially a surface-water form. They record it from the surface on several occasions and give its lower limit as about 100 fathoms. Only a few isolated specimens were taken from greater depths (500 and 750 fathoms).

It is not expected that normal variations in temperature and salinity will be shown to have any appreciable effect on the vertical distribution of this species, as it has been observed to live under a wide range of conditions as regards both these factors (range of salinity 2–35 °/oo, limits 1·53–35·4 °/oo : range of temperature 6–18 deg. C., limits 1–22·6 deg. C), but until more data are available it is impossible to discuss this point or to consider differences between its diurnal and nocturnal distribution in relation to depth.

TABLE I

Weather Conditions during 1928 Plankton Cruises.

Date.	Wind.	Sea.	Visibility.	Remarks.
Aug. 20th	N.E.	E. ; strong	Poor ; rain	Too rough for work.
,, 21st	,,	,,	,,	,, ,,
,, 22nd	N.	N.E. moderating	Poor	
,, 23rd	S.S.E. ; light	Moderate	,,	
,, 24th	Increased	" Hashy "	Poor ; rain	
July 25th	W. ; light	Smooth	Very good	Visibility exceptionally good throughout trip — coast seen from off-shore stations.
,, 26th	,,	,,	,,	
,, 27th	Light ; variable	Light N. swell	Good	
,, 28th	Light ; N.-N.W.	,,	Cloudy, rain	
June 22nd	Fresh, W.		Moderate.	
,, 23rd	Strong, W.		Better.	
,, 24th	Fresh-strong		Good.	
June 1st	Light, S.E.	E. swell.		
,, 2nd	Light, N.	Haze, clearing later.		
April 24th	Fresh, S.		Moderate.	
,, 25th	,,	S.E.	,,	
,, 26th	Light, N.E.	Calm	,,	

PART II. THE LIFE-CYCLE OF *EVADNE NORDMANNI.*

1. The Parthenogenetic Phase.

The paired ovaries of *E. nordmanni* are small, spindle-shaped structures lying at the sides of the intestine. The posteriorly directed end of the ovary is rounded while the opposite end may be drawn out to a fine point.

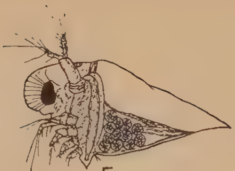
After the eggs have been shed into the brood pouch, the ovary is invisible in stained preparations (Figs. 5 and 11), but, as the embryos develop, the organ is again discernible, its contents developing meanwhile so that by the time the embryos are ready to be freed, a second generation of eggs has been formed and may be extruded even before the previous batch of embryos has been set free. (Figs. 6–9 and 14.)

As the preparations examined were made from material not specially preserved for the purpose, it has not been possible to make out the details of the early development of the ovarian cells—the nuclei not being visible. In the earliest phase in which the ovary can be seen, it is filled with a mass of tissue not shown to be definitely marked off into cells. Later a number of irregularly shaped cells are closely pressed together in all but the narrow anterior end of the ovarian sac, and finally the same space is occupied by a string of large cells varying in number from four to six or rarely eight. The last of these is placed at the extreme posterior end of the organ, while the anterior part is now filled with a group of very small cells (Figs. 15 to 18). The anterior part of the ovary thus evidently constitutes the germarium described by W. F. R. Weldon (**84**) as occupying this position. The posterior end of the ovary is turned towards the dorsal side of the body and, at the time of egg extrusion, no doubt forms a short oviduct which becomes continuous with the wall of the brood sac as suggested, though not actually seen, by Claus (**12**).

In certain preparations only four large ovarian cells are present and there is no germarium. As this condition occurs in specimens bearing only very few embryos, indicating the condition of depression already mentioned as preceding the sexual phase, it would appear to be an early stage in the formation of the resting-egg (Fig. 34). This will be discussed below.

The process of development of the parthenogenetic eggs of Polyphemidae was described originally by Claus who stated that the tetrad-formation of ovarian cells, which undoubtedly occurs in the production of the gamic egg, occurs also in the development of the agamic generations—one cell from each tetrad giving rise to an ovum, the others serving as "nurse-cells" or feeding cells for its nourishment.

Kuttner (**33**), on the other hand, states that never was the tetrad formation observed, that no "nurse-cells" are present and that each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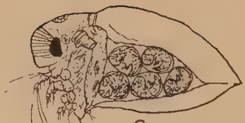
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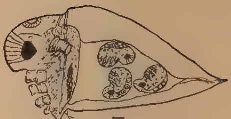
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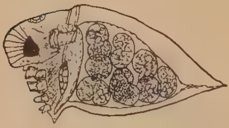
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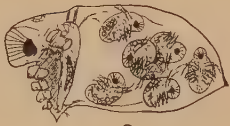
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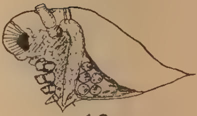
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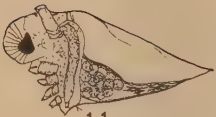
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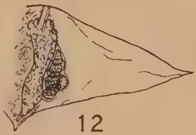
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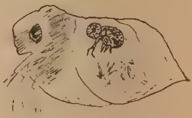
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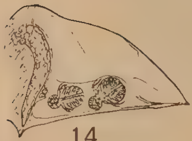
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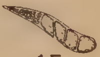
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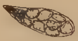
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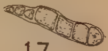
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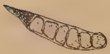
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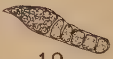
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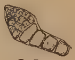
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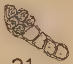
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FIG. 5.—Parthenogenetic female of *E. nordmanni* with embryos in blastula stage. Shows thickening of anterior wall of brood pouch and cells suspended in cavity towards apical end.

FIG. 6.—Developing embryos in brood pouch; ovary again becoming visible.

FIG. 7.—Brood pouch containing well-advanced embryos bearing eggs. Maternal ovary further developed than in preceding figures.

FIG. 8.—Female showing conditions during height of parthenogenetic activity; nine embryos in brood pouch. Ovary with seven egg cells and germarium.

FIG. 9.—Fertile embryos in shell cavity ready for freeing. Shows torn walls of brood pouch.

FIGS. 10 and 11.—Brood pouch with eggs; shows its relatively small size at this stage and the glandular cells of its wall, as in Fig. 5.

FIG. 12.—Newly extruded eggs in very small brood pouch with glandular cells not yet visible.

FIG. 13.—Cast cuticle containing one embryo and what appear to be cuticles of two others in shell cavity.

FIG. 14.—Brood pouch containing two fully-formed embryos and enclosing second very small brood pouch with two newly extruded eggs. Here, as in Figures 9 and 13, the embryos are free from the egg membrane.

FIGS. 15, 16, and 18.—Ovaries with varying numbers of egg cells in posterior portion; anterior end occupied by germarium.

FIGS. 19 and 20.—Ovaries including egg cells and large germaria with cellular contents.

FIGS. 17 and 21.—Most advanced stage in development of ovaries, i.e. with two generations of germ cells. (Taken from preparations of specimens with several embryos in brood pouch.)

germ cell develops independently and produces an egg. This is evidently a fact in regard to the large cells which come to occupy the more posterior part of the ovary towards the end of the period of embryonic development of the previous batch of eggs, but it may well be that each of these is the product of one of a group of four small cells produced by the germarium as stated by Weldon. He described proliferation in the germarium as giving rise to quadri-nucleate masses which form four cells, one of which becomes an ovum and is nourished by the others, which then die. As already stated, the preparations do not show the details of these earlier stages at all clearly, but are good enough to indicate that the ovary contains more protoplasmic masses or cells at the earlier stages than there are large egg cells present when these are fully grown (Figs. 19 and 20). During the active period, when many embryos are produced, the germarium may occupy more space than the remainder of the ovary and its contents are definitely cellular. This is shown in Figure 21.

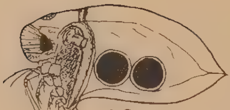
The failure of Kuttner to observe the germarium may be due to the examination of specimens nearing the end of the parthenogenetic period, or to mistaking it for the anterior end of one of the chain of egg cells from which it is sometimes difficult to distinguish it.

The presence of young germ cells and fully-formed eggs in the ovary, together with advanced embryos in the brood pouch, is interesting in that four generations of individuals may thus be seen together in different stages of development. This, taken along with the fact that the embryos also become fertile before leaving the brood sac, furnishes an adequate explanation of the rapid and enormous increase in numbers of individuals which takes place under conditions favourable to parthenogenetic reproduction.

Kuttner mentions the fact of the embryos being fertile as significant in regard to the recording of no females with empty brood sacs, but the two stages of cells in the ovary is equally important in this connection. Nevertheless, females with empty brood sacs have been observed. This occurs at the end of the agamic period and appears to be a necessary preliminary to the preparations for the nourishment of the sexually formed "winter-egg."

Claus has described the brood pouch as a closed feeding-chamber or "uterus" in which the embryos are nourished from the maternal circulation through the medium of the glandular cells of its wall and states that the feeding area is further increased by an infolding of the anterior wall by means of which glandular cells are suspended within the cavity of the brood chamber.

Kuttner's crudely figured "Blasenförmiges Organ" is shown as a band of large square-sided cells passing across the middle of the brood chamber. Nothing like this has been seen in the Northumberland material, which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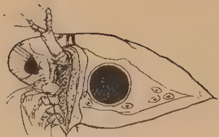
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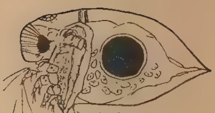
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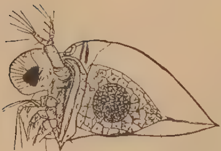
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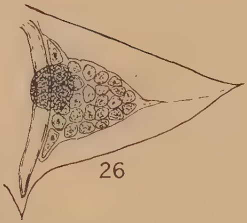
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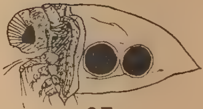
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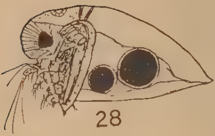
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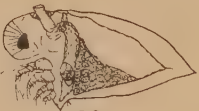
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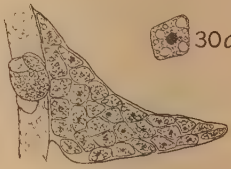
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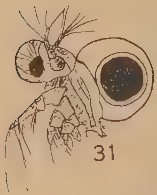
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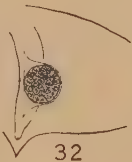
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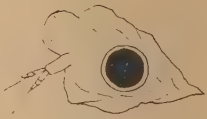
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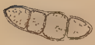
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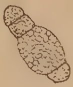
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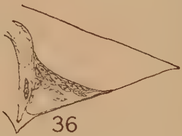
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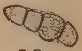
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Fig. 22.—Female *E. nordmanni* with two fully-developed winter-eggs of equal size in brood pouch. Nurse-cells entirely disappeared.

Figs. 23 and 24.—Winter-eggs almost or completely developed, with thick shell. Shrunken remains of some nurse-cells in brood sacs.

Fig. 25.—Developing winter-egg within closely packed mass of nurse cells. Protective shell not yet begun to be formed.

Fig. 26.—Rather later stage than last—nurse-cells less numerous and less closely packed.

Fig. 27.—Two fully-formed winter-eggs escaping through ruptured wall of brood pouch into shell space.

Fig. 28.—Specimen containing two winter-eggs of unequal size.

Fig. 29.—Young winter-egg surrounded by other three cells of the tetrad. Brood pouch already filled with nurse-cells.

Fig. 30.—Detail of Figure 29 more highly magnified.

Fig. 30a.—One of glandular nurse-cells enlarged to show nucleus, fat globules and granules.

Fig. 31.—Specimen of *Podon ? polyphemoides* with winter-egg in shell cavity.

Fig. 32.—Growing winter-egg of *E. nordmanni* showing formation of envelope. (Brood sac and nurse-cells not indicated.)

Fig. 33.—Cast shell of Evadne containing a winter-egg.

Fig. 34.—Earliest stage in winter-egg formation observed. Ovary contains only a tetrad with third cell slightly enlarged but not noticeably different from others in texture.

Fig. 35.—Rather later stage than last. Third cell now definitely larger and filled with fat globules.

Fig. 36.—Stage between those shown in Figures 34 and 35. Brood pouch formed and partially filled with nurse-cells which are situated chiefly along its anterior wall.

Fig. 36a.—Shows detail of ovary shown in Figure 36. Third cell of tetrad filled with fat globules.

shows, during certain stages of brood sac formation, a condition similar to that described by Claus.

When the eggs first leave the ovary they lie at the posterior end of the shell cavity, just anterior to the caudal furca and closely surrounded by a fine membrane which forms the wall of the brood sac (Fig. 12). The eggs are thus pressed together and are not circular in outline as they become later. As the eggs develop, the wall of the brood pouch correspondingly expands and its cellular character becomes obvious. It is attached to the shell along its posterior border and becomes triangular in shape. The anterior wall appears thickened, and elongated spindle-shaped cells occupy the apex of the triangle (Figs. 5, 10, and 11). With further development of the embryos, the brood pouch lengthens until its attachment consists of a fine strand of tissue connecting its end with that of the shell (Fig. 6). When the brood sac contains only a small number of embryos its shape is not conspicuously altered, but when packed with many well-grown young its anterior side becomes rounded and it occupies a considerable portion of the shell space which is correspondingly altered in shape (Figs. 8 and 9).

As the development of the embryos nears completion the glandular cells of the brood sac wall are no longer visible (Fig. 7). When the young are fully formed and ready to be freed they are evidently capable of individual movement within the brood sac and the thin wall becomes ruptured, permitting their escape into the shell-space (Fig. 9).

From the torn appearance of the brood pouch after the embryos have passed out and from its very small size when the eggs first reach it, it appears to be used only once and renewed for the reception of each successive batch of eggs. Claus, quoting Lovén, mentions the immediate contraction of the walls of the brood pouch on the exit of the embryos, but that this does not occur invariably is evidenced by the torn remains of its walls visible in our preparations, and by the fact that a new batch of eggs may leave the ovary and be surrounded by a second tiny brood pouch while the embryos of the previous generation are still retained within theirs (Fig. 14).

That the complete freeing of the embryos takes place in two stages, as described by Lovén, is shown even from a study of fixed material. Following the first stage already described, the final freeing from the maternal shell space is brought about by ecdysis of the mother, when the embryos remain in the old shell, from which they can then make their escape.

Discarded shells containing one or more embryos have been observed as well as stages following the rupture of the brood pouch. One preparation, illustrated in Figure 13, shows a cast shell in which one embryo is retained together with what appear to be the cast cuticles of two other embryos, indicating that the young cast their skins at or about the beginning of their free existence. This is probably their first ecdysis, as the embryos are retained within the egg membrane during the greater part of their sojourn within the brood sac.

The number of embryos in a batch may vary considerably. That both ovaries shed their eggs simultaneously and that each of the large ovarian cells may, under favourable conditions, produce an embryo, is seen from the presence of as many as fifteen blastulæ and up to thirteen or fourteen advanced embryonic stages. (It is difficult to be sure of the exact number when so many embryos are packed together in the brood sac.) The usual number, however, is not nearly so large—generally six to eight or nine—while at times the majority of specimens carry only two to five embryos. An analysis of the samples taken at different periods shows this condition to be coincident with the several stages of the parthenogenetic phase. Ordinarily, during the period of more active metabolism, larger numbers of young are produced, while the depression mentioned as preceding the onset of the sexual phase is indicated by the presence of fewer embryos, as well as by the occurrence of males in the samples.

The number of embryos formed is, in the first place, dependent upon the number of ripe germ cells in the ovary, but it is apparent that it may be further regulated, especially towards the end of the agamic period, by some of these failing to develop. Although it has not been possible to demonstrate the fate of these cells, it is believed that they disintegrate before leaving the ovary, as batches of newly extruded eggs may consist of only two (Fig. 14).

The greatest number of embryos, i.e. twelve to fourteen, has been observed only in the large form of *E. nordmanni*, referred to as occurring occasionally among the ordinary population. As regards the others, carrying from two to nine or more young, there is no appreciable difference in body-size, although those containing large well-filled brood pouches have the shell distended into a more rounded contour instead of the typical triangular form of less heavily burdened specimens, thus making the body appear more bulky.

The progressive decline in activity during the parthenogenetic phase, here shown for *E. nordmanni*, as indicated by the decrease in the number of embryos produced, provides an explanation of the discrepancies between the accounts of various authors as to body shape and number of young borne by this species. In consequence, as noted above, it has been regarded as having a North Sea variety which produces seven or eight eggs and a Baltic variety with two to five. Also Claus, who examined Mediterranean specimens in September, gives the number of embryos as four to six. That he was dealing with material nearing the end of the parthenogenetic phase is evident, not only from the time of year when the specimens were taken, but also from his account of developing winter-eggs obtained at the same period.

The number of eggs in the first batch produced by a female while still in the maternal brood pouch apparently varies within only small limits. Claus gives the number as four to six. Kuttner figures an embryo bearing five blastulæ, and our material also gives examples varying from four to six eggs or blastulæ.

The presence of males was noted towards the end of the parthenogenetic period, but there are no special observations to record. They are readily distinguishable from the females by the absence of a brood pouch and by the rounded form of the paired testes which are easily discernible in stained preparations.

2. The Sexual Phase.

Claus' observations on the development of the winter-egg, which are incomplete due to lack of material, are here confirmed. There is no question as to the production of the gamic egg from one of a group of four ovarian cells as described by him, but our material includes quantities of females with such eggs in various stages of development, and a fuller account of the process is now possible.

The earliest stage seen shows the ovary to contain only four large cells arranged in a row, the third from the anterior end being already slightly broader than the others. No germarium is visible, the ovarian wall being closely apposed to the edges of the tetrad (Fig. 34). That this is an early stage in winter-egg production is indicated, as already stated, by the absence of the germarium, the size of the third cell and by the fact that the brood pouch contains only one embryo which appears to be a male as, although fully developed, it bears no eggs beneath the cuticle on its dorsal side.

There is at this stage no indication of the presence of the nurse-cells which later occupy the brood pouch prior to its reception of the growing winter-egg.

Claus noted the absence of any other cells in the ovary during the formation of the winter-egg and assumed therefrom that other oocytes formed at the same time as the one that gives rise to the tetrad must have passed out to become the glandular nurse-cells which nourish the growing egg in the brood sac. An examination of our material, however, shows the nurse-cells to have a different origin.

In the stage shown in Figure 34 the future winter-egg has the same granular appearance as the other three cells of the tetrad and is only distinguishable by its slightly larger size. There is no sign of the formation of the brood sac or of the presence of glandular cells. At a slightly later stage, that illustrated in Figures 36 and 36a, the winter-egg has assumed its characteristic appearance of being filled with globules of fat, and a brood pouch of moderate size has been formed. This contains a number of nurse-cells which partially fill it, and they, for the most part, are situated along its anterior border. That is to say that they arise in the same position as do the glandular cells present during the development of the parthenogenetic embryos. This would seem to indicate, in the absence of any other cells capable of nourishing the egg, that they are not derivatives of ovarian cells at all, but are actually the product of the wall of the brood pouch, arising, as in the former case, from an invagination of its anterior border. That they become markedly different from the cells which feed the parthenogenetic embryos in size, shape, number and contents will be seen by a comparison of Figures 5, 10 and 11 with Figures 25, 26, 29, and 30.

The slightly older stage shown in Figure 35 is drawn from a specimen in which the brood pouch is still only partially filled with nurse-cells; but when the stage represented in Figures 29 and 30 is reached and the egg, while retaining its original position, has increased in diameter to about the width of the intestine, the brood pouch has become packed with thirty to forty large glandular cells, polyhedral in shape through mutual pressure and having the appearance indicated in Figure 30a. A central nucleus is present, and a number of fat globules of various sizes are to be seen in the granular cytoplasm.

As the egg increases still more in diameter, a fine membraneous envelope appears, surrounding it closely on its dorsal side and drawn away from it ventrally, as shown in Figure 32, suggesting that it is the product of the ovarian wall. The three cells associated with the young winter-egg have now disappeared.

During the subsequent growth to its relatively enormous size the egg does not as a rule become far removed from the region of the ovary, but lies embedded, at the proximal end of the brood sac, in the mass of nurse-cells which now fill it. When, however, two eggs are developed simultaneously, one is placed more distally (Figs. 22, 27, and 28).

From the first appearance of fat globules in the egg, when it loses its ability to take up stains readily absorbed by the remainder of the body, and particularly the nurse-cells, it becomes difficult to distinguish, especially when it has come to be situated within the brood chamber. Due to this and the fact that the closely packed mass of nurse-cells may have the appearance of a large number of early embryos, it was not until a considerable quantity of material had been examined that the significance of these cells was appreciated and their presence in the brood pouch was found always to be coincident with the occurrence of a winter-egg in process of development.

As the winter-egg nears its limit of growth the nurse-cells decrease somewhat in size and number and become more sharply separated from one another (Fig. 26). The thick protective shell is then formed and when the development is completed a few shrunken remnants of the nurse-cells may still be present, as shown in Figure 23. When two eggs have been formed the brood sac is generally empty.

The fully-formed resting-egg breaks through the wall of the brood sac and lies in the maternal shell cavity. There is no production of an ephippium in Evadne, the winter-egg being simply left in the cast shell on the subsequent ecdysis of the mother. As cast shells containing winter-eggs have been taken in the plankton samples on several occasions (Fig. 33), it is possible that they do not immediately sink to the sea bottom as previously supposed and that, in the case of those formed in early summer, they may perhaps remain planktonic and develop comparatively rapidly without a marked resting period.

While the production of a single winter-egg is to be regarded as the normal condition, it is by no means rare to find two present—evidently one from each ovary—especially during the summer sexual period. When this occurs, the eggs may be sub-equal in size, both considerably smaller than the fully-grown single egg (Fig. 22), or they may be markedly different in size (Figs. 27 and 28).

A study of Geoffrey Smith's work (**73**) on the storage of glycogen and fat by Crustacea led to the making of preparations stained with neutral red and with osmic acid. As the material used was by no means ideal for the purpose, it was not expected to give particularly good results, but they were sufficiently convincing to be worthy of brief reference.

The osmic acid preparations showed the developing winter-egg to be more heavily loaded with fat than any other part; also the nurse-cells and the gut took up the stain fairly strongly. Specimens carrying embryos showed a certain amount of fat to be present in these, but the neutral red preparations indicated that it is glycogen which is the predominating substance stored during the parthenogenetic phase. It is present at the bases of the limbs, in and about the intestine, and is particularly obvious in the ovaries (especially the germarium), and in the contents of the brood sac. Indeed, the neutral red served as a differential stain for the ovaries, showing up their contents as did none of the general stains previously used—such as borax carmine, alum cochineal, and methyl green.

Specimens in the sexual phase, treated with neutral red, showed glycogen to be present in the ovary during the tetrad formation, all four cells being deeply stained at first, but the young winter-egg ceases to take up the stain as soon as fat globules appear within it and thereafter remains unstainable. Some glycogen is present in the nurse-cells in addition to the fat, and also in the intestine.

These facts show that *E. nordmanni* behaves similarly to other Crustacea which have been investigated as regards alternating periods of fat and glycogen storage associated with the periods of sexual activity and of growth respectively.

The most interesting and striking feature of the analysis of the Northumberland material is the evidence of a definite double cycle in the annual history of marine Cladocera as shown for *E. nordmanni.* Except for Apstein, who touches briefly on the subject, no previous attempt has been made to work this out, to compare marine with freshwater forms in this respect or to correlate the phenomenon with environmental conditions.

General Conclusions.

The very considerable amount of work which has been done on the investigation of the life-cycle of Cladocera in relation to environmental conditions and to hereditary qualities, has been carried out almost entirely on freshwater forms. Observations on these under natural and experimental conditions have led to widely different theories as to the probable causes of the change from parthenogenetic to sexual activity.

Weismann was of the opinion that there is a definite inherent cycle which causes the production of a particular number of gamic generations —the number varying with the species—between every two gamic periods, regardless of external changes. On the other hand, the generally accepted idea has been that the life-cycle is intimately bound up with seasonal variations in the environment, and that the production of winter-eggs occurs at the onset of conditions unfavourable to continued activity of the organism, i.e. that in nature it precedes hot dry periods when small bodies of water are liable to become dried up, and cold spells when freezing may occur.

With regard to the effect on the organism of these conditions it is obvious that it is not the actual process of desiccation or freezing which brings about the development of the protected resting-egg, for to be of any value in preserving the species, its formation must be completed before the unfavourable conditions supervene, and the stimulus to sexual reproduction must be looked for in changes which take place some little time in advance.

If physical factors of the environment are regarded as being mainly responsible for changes in metabolic activity of the organism, it is necessary to consider what these are and to attempt to discover how they act. The more obvious changes are those of temperature and salinity* and, having regard to climatic conditions in various parts of the world, it is evident that species living in different climatic zones may react differently if these factors exert a direct influence. That is to say that the gamic phase may be associated in some cases with an increase in the amount of the factor or factors concerned and in other cases with a decrease in the amounts of the same factors.

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* A detailed discussion of the effects of normal variations in the percentage of dissolved oxygen and carbon dioxide and in the amounts of different chemical compounds present in the water is regarded as unnecessary. Such variations will not ordinarily be of sufficient magnitude to act as direct limiting factors of the activities of epiplanktonic animal forms of open waters, with which the present discussion is primarily concerned. A knowledge of these and of their indirect effect is assumed in the following consideration of changes in abundance of the phytoplankton in its relation to the nutrition of Cladocera.

Due to the occurrence of large swarms of Cladocera which have been observed to congregate in restricted areas (even in large lakes) during the agamic period, two other factors have been regarded as of importance, namely the accumulation of excretory products and the possible scarcity of food, or changes in the constitution of available food material. The question of nutrition is of vital importance both as a direct factor and in its relation to physical changes, notably temperature, as stimuli influencing both the amount of food material obtainable and the organism's ability to use it.

Experimental work prosecuted with a view to determining the value of various physical and nutritional factors believed to be instrumental in bringing about the cessation of parthenogenesis, has resulted in many and conflicting conclusions. This experimental work has been summarised by Cutler (**14**) and more recently and completely by Schull (**63**), whose comprehensive and critical account makes it unnecessary to discuss it here.

As regards the theory of the inherent cycle in Cladocera, first formulated by Weismann and attributed to the effect of natural selection, there is again considerable difference of opinion resulting from more recent investigations. Papanicolau (on showing that early broods are strongly parthenogenetic in tendency, late broods gamic in tendency and intermediate broods easily influenced either way) assumed the existence of a graduated inherent cycle, but his results can also be interpreted in the light of changing environment, as shown by Agar (**1**) and others. Also Banta, having reared three hundred generations of Moina, found it no easier to induce the gamic phase then than in early generations.

Woltereck (**86**) takes the *via media*, being of the opinion that internal and external causes are equally contributory to the production of gamic forms. While retaining the idea of internal stimulus to periodicity and postulating the presence of " paralisators " and " activators " within the organism, acting in opposition to one another to produce alternating phases of its life-cycle, he permits these hypothetical substances to be set in operation by the action of physical factors of the environment.

That there is here an inherent cycle in the sense that periods of rapid somatic growth, of reproductive activity, and of comparative rest are characteristic of Cladocera as of living organisms generally, is obvious, but data relating to the behaviour of particular species in different types of natural habitat show plainly that nothing more need be claimed regarding the part played by heredity and natural selection. The work of Zschokke and of Ekman has demonstrated that a particular species of Cladocera may be dicyclic, polycyclic or even acyclic in varying freshwater conditions presented on the European plains, but is strongly and definitely monocyclic in high Alpine lakes and in lakes and ponds of the far North.

Beyond the fact that gamic reproduction must occur at some period (except possibly in "acyclic" forms), it is evident that the stimulus which induces the gamic phase must be sought in those environmental factors which necessarily limit or accelerate, directly or otherwise, the rate of metabolism of the organism at any given time. This would appear to be the idea behind von Scharfenberg's attempt to reconcile the two opposed views regarding the relative importance of internal and external factors, by assuming that the influence of food on the cycle is an inherited quality acquired through natural selection.

With regard to the conclusions drawn by various workers from the results of their experiments, one or two points appear to be worthy of further mention. Much has been made of the effect of the accumulation of excretory products, resulting from overcrowding, in inducing gamic reproduction (or at least depression), but it seems to the writer that this must be of far less consequence in nature than under experimental conditions. That it is probably a contributory cause of depression in small or in very stagnant bodies of fresh water at times of maximal population is not denied, but that such an accumulation can occur to any marked extent in large water masses, whether of fresh water or the sea, where there is considerable movement, at least near the surface, the writer is unable to appreciate. Also, in so far as carbon dioxide is to be regarded as an important excretory product in this respect, it might with equal probability be assumed to have the reverse effect in that it would tend to increase the supply of phytoplanktonic food-material.

Geoffrey Smith's experiments on the effect of temperature also call for remark in the light of our observations on Evadne. He states that a lowering of the temperature, which induces gamic reproduction, acts as a stimulus to the storage of fat in the tissues as opposed to glycogen. That decreased temperature need not be operative, or is not the only stimulus regulating fat storage, is shown by the incidence of the gamic phase in Evadne at two different seasons—one when the temperature is rising prior to its August maximum value and the other usually when this is well past. Similar conditions obtain in regard to salinity in the case of Evadne, the first gamic phase occurring about or before the period of the annual maximum, the second considerably later.

The fact that the question of food-supply has generally been considered of vital importance is brought out, as noted by Schull, by the event of more experimental attempts having been made to connect the life-cycle with nutrition than with any other external factor—temperature being a close second. As decreased temperature is generally regarded as acting either through its effect on the amount of food-material available or in reducing the rate of the organism's metabolic activity and consequently lessening the nutritive process, it may be assumed to be an important contributory factor in nature at those times at which low temperature and depression or the occurrence of the sexual phase supervene simultaneously. This does not however take into account those times when gamic individuals occur also during periods of comparatively high temperature.

It was evidently this difficulty which led Keilhack, arguing from observations in nature, to reject the idea of low nutrition as an important factor in the production of sexual forms. He remarks that *Polyphemus pediculus*, a dicyclic form, has a gamic phase in June "when food is abundant." His contention is supported by Strohl who states that a gamic phase in June could not be due to lack of nutrition. As to the abundance of food suitable to continued asexual activity of dicyclic Cladocera at these times, there must be considerable doubt and, from a study of recent work on the periodicity of freshwater Cladocera together with our records for Evadne, this contention must definitely be rejected.

From observations in the field, the general conclusion of Dr. Robert Gurney, with whom the writer has been in correspondence, is that shortage of food is the main direct limiting cause of the cessation of parthenogenetic development of freshwater Cladocera, as it appears to be in the case of marine species also. Leaving aside the special problems relating to food-supply in temporary ponds and the like, and in lakes situated at high altitudes and high latitudes where, compared with permanent water-masses of temperate regions, the periods suitable to food production are of relatively short duration, the periodicity of abundance and scarcity of food is closely parallel in both marine and freshwater habitats.

It will be sufficient here to draw attention to the similarity in number, times of appearance and relative productivity of the periods of maximal abundance of the phytoplankton of fresh and sea-water, without entering upon a detailed discussion as to the causes of the same, and to show the close relationship between these and the life-cycles of characteristic Cladoceran inhabitants. It has generally been supposed that marine Cladocera were monocyclic and that their activities, therefore, bore no relation in respect to periodicity, to limnetic forms. Also, as it is only comparatively recently that the dicyclic character of the latter has been correlated with changes in abundance of phytoplankton, no comparison has been drawn between fresh water and marine Cladocera in this respect until now.

Taking into consideration regions in which temperate climatic conditions obtain, a similar periodicity of phytoplanktonic activity is found to occur in freshwater lakes and in the sea. In the former the two periods of upheaval caused by temporary full circulation of the water in spring and autumn due to the development of a thermocline (and in certain cases to other causes as in Lough Derg) (**74**), give rise not only to the provision of nutritive substances required for the rapid multiplication of diatoms, green algæ, etc., but also bring increased supplies of food-material directly within the reach of detritus feeders among the animal plankton such as are many of the freshwater Cladocera. Thus, two periods of reproductivity of the zooplankton are possible. While this may be associated in some species with the one, in others with the second period of optimal nutritive conditions, certain forms such as Cladocera and Rotifers may take advantage of both periods (**11**) : here the agamic phases are coincident in time with both the aforesaid periods and thereafter the population suffers a reduction in numbers followed by the sexual phase.

In the sea, a similar series of events takes place, the spring and autumn maximal periods of parthenogenetic development of Cladocera being associated in time, at least in a general way, with the corresponding periods of diatom abundance, after which numbers decline and the gamic phase supervenes. This has been shown for *E. nordmanni* to be more strongly marked after the spring maximum than it is in autumn, thus indicating an association between Cladocera and phytoplankton in regard to relative quantity as well as to time. Another aspect of the effect of varying quantities of food on Cladocera, while not having a direct bearing on the present problem, is nevertheless interesting. Wolterek (**88**), in his recently published book, shows the possibility of inducing modifications in the form of *Daphnia cucullata* in response to abundance or scarcity of food.

That there is a definite relationship between times of food scarcity and corresponding periods of depression in the metabolic processes of plankton organisms generally is now evident. It has been shown by Dieffenbach and Sachse, as quoted by Carpenter ; is suggested by the findings of Gurney (**24**), Zschokke, and Ekman referred to above ; is indicated in the analysis of samples taken by Scourfield (**70** and **71**) and is of common occurrence among marine planktonic forms. In addition to being demonstrated in the case of Evadne, the Northumberland plankton samples show the presence of spring and autumn periods of reproductivity in the common acorn barnacle (not yet worked out in detail), as is the case in many holoplanktonic forms and littoral animals with pelagic larvæ, e.g. Mysis spp., *Crangon vulgaris* (**6**), *Sagitta elegans* (**47**).

The emphasis laid on the influence of the vernal and autumnal maxima of phytoplankton on the zooplankton generally and on limnetic and marine Cladocera in particular, is meant to detract in no way from the importance of the physical factors of the environment but is meant to draw a comparison between the similarity of the more important features regulating the cyclic activities of both marine and freshwater pelagic animals, and to draw attention to the effect of physical changes being generally indirect rather than direct in their influence. There is, of course, no question of the direct effect of decreased temperature, for example in lowering the rate of nutrition ; but so far as dicyclic Cladocera are concerned this is a secondary stimulus, brought to bear on the autumnal period of depression but not on the spring one.

As regards the results of experimental and other observations on the influence of increase or decrease in the intensity of physical and nutritional factors, it would appear that it is not necessarily or only the actual amount of any particular factor which affects the organism concerned, but rather " change as change." This is pointed out by Schull in reference to Whitney's work, and its importance in regard to the constitution of the available food-supply is shown by von Scharfenberg's experiments. That his conclusions are confirmed by the behaviour of plankton organisms in nature is indicated by the fact that while the spring increase of diatoms is followed by abundance of Peridiniæ in the summer, agamic reproduction in dicyclic Cladocera nevertheless comes to an end (or at least is greatly slowed down) and supervenes again at a rapid rate only when the diatom curve is once more on the up-grade in early autumn.

While the Northumbrian records of periodic abundance of Evadne show it to follow the trend of the general annual diatom curve, there is considerable variation in the times of maximal population from year to year, and it is not yet possible to show to what extent these variations are coincident with minor changes in the position of the cusps of the diatom curves in those years in which abnormal conditions have prevailed in the region under consideration.

SUMMARY.

PART I.

From an analysis of previous records of *E. nordmanni*, considered in conjunction with those furnished by the present investigation, the following points of interest emerge.

1. *E. nordmanni*, while being generally distributed in the North Sea and adjacent waters throughout the summer months, has been shown to breed freely in inshore waters in early summer and again in autumn when maximum numbers of individuals are obtained.

2. These two periods of maximal abundance are produced as the result

of successive parthenogenetic broods and alternate with periods of depression. This is indicated not only by the sexually-produced winter-egg, but also by a reduction in the number of embryos contained in the brood chamber and consequent change in body-shape. This serves to show that the supposedly distinct races, described as being characteristic of the North Sea and the Baltic, have no doubt been founded on material taken at different periods of the agamic phase.

3. The alternating periods of abundance and scarcity appear to be associated with transnatant movements of the population.

4. The earlier maximum is the more extensive one and the following period of scarcity of numbers in inshore waters is less marked and of shorter duration than that which follows the autumn maximum. Although the Northumberland records do not cover a sufficient number of months of any year to provide information as to the presence of *E. nordmanni* during the winter, it is evident from previous accounts that a certain proportion of the population is able to withstand both periods of depression and that these, together with new individuals produced from the resting-eggs and others entering the area from without, provide a stock from which the following early summer maximum is obtained.

5. The distribution of the species is affected by exceptional conditions wrought by changes in the current system of the area of distribution.

6. *E. nordmanni* is an inhabitant of both coastal and oceanic waters. It is present in great quantity on both sides of the North Atlantic, and it is suggested that its geographical distribution is intimately associated with the current system of that ocean. Its distribution beyond this region is merely indicated.

7. A comparison of the surface current systems of the southern North Sea, the Irish Sea, and the eastern English Channel is made in an attempt to explain the scarcity of Cladocera in these regions.

8. The material available for the study of the vertical distribution of Evadne is adequate to illustrate only diurnal conditions and shows the optimum light intensity to be very high for this form. There is no evidence that Evadne retires below the surface to any noticeable extent in rough weather.

PART II.

9. The account of the development of the parthenogenetic generations of *E. nordmanni* has reference to the formation of the oocytes; the development of the brood pouch and the production of the nutritive cells of its wall; the method of freeing of the embryos.

10. The presence of three generations of young within the mother and the fertility of the embryos are considered in relation to the rate of

increase of the population. The variation in number of embryos within the brood pouch is discussed in its association with the period of depression which is shown to precede sexual reproduction. The fact that the brood pouch may at times be empty is shown, and is correlated with the change from the agamic to the sexual mode of development.

11. A more detailed description of the formation and growth of the winter-egg than has been given heretofore is included, and has reference to the formation of a tetrad ; the disappearance of the germarium ; the production, derivation, constitution, and absorption of the nurse-cells and the freeing of the winter-egg. The significance of the production of two winter-eggs simultaneously is considered.

12. Evadne is shown to behave similarly to other Crustacea in the matter of fat- and glycogen-storage, being associated with alternating periods of active growth (parthenogenetic phase) and gamic reproduction.

13. The general conclusions arising out of the study of the life-cycle of Evadne which shows it to be definitely dicyclic, are concerned with the question of the relative value of internal and external factors as stimuli effecting the biannual series of changes which occur, and it is believed that food-supply is of primary importance and that other factors are of a secondary nature or are indirect in their influence.

14. A coincidence of the periods of maximal population of Cladocera with those of diatom abundance is shown to take place as regards both time of occurrence and relative productivity. A comparison is drawn between the behaviour, in relation to food-supply, of marine and limnetic species of Cladocera.

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Studies on the Monogenea of Plymouth. *Gastrocotyle trachuri* v. Ben. and Hesse, 1863.

By

By E. Idris Jones, B.Sc. (Lond.)

With 4 Figures in the Text.

In August, 1932, six specimens of this species were found on the gills of *Trachurus* [*Caranx*] *trachurus* taken at Plymouth. This is the first record of its occurrence in British waters.

The genus and species were first defined by van Beneden and Hesse (1864), their description being from young specimens, and incomplete in numerous details. No account of the internal organs is given, the genital opening is not described and the number of crotchets or hooks at the posterior end of the body is said to be four. This undoubtedly arises from the fact that their specimens were immature, being 1·5 mm. in length, whereas the specimens found at Plymouth are *circa* 4·7 mm.

Of subsequent authors Taschenberg (1879, a and b) refers to Gastrocotyle, but depends on van Beneden and Hesse's description and adds no new details. J. T. Cunningham (1887) refers to Gastrocotyle in a discussion on the systematic position of Stichocotyle, but again contributes no new details. Monticelli (1888) discusses its systematic position, depending on van Beneden and Hesse's description ; von Linstow (1889) mentions Gastrocotyle in his Compendium, but the first record of its occurrence after van Beneden and Hesse's discovery comes from Paroni and Perugia (1890, a) who found it on the gills of *Trachurus trachurus* at Genoa and later in the same year (1890, b) published a description of the species. This account is a big advance on that of van Beneden and Hesse, but is still incomplete. The reproductive organs are said to be similar to those of Microcotyle, but no description is given. Six crotchets are described at the posterior end of the body and the cotylophore bears 35 suckers. The measurements of their specimens are 3 mm. × 1 mm. Unfortunately the armature of the suckers is not figured. Braun (1893), Pratt (1900), Monticelli (1903), Nicoll (1915), and Brown (1929) all make references to the species, but no new data or records are added.

The specimens here described were found during an investigation at Plymouth on the trematodes of fishes. During this investigation it was repeatedly noticed that when copepods were present on the gills

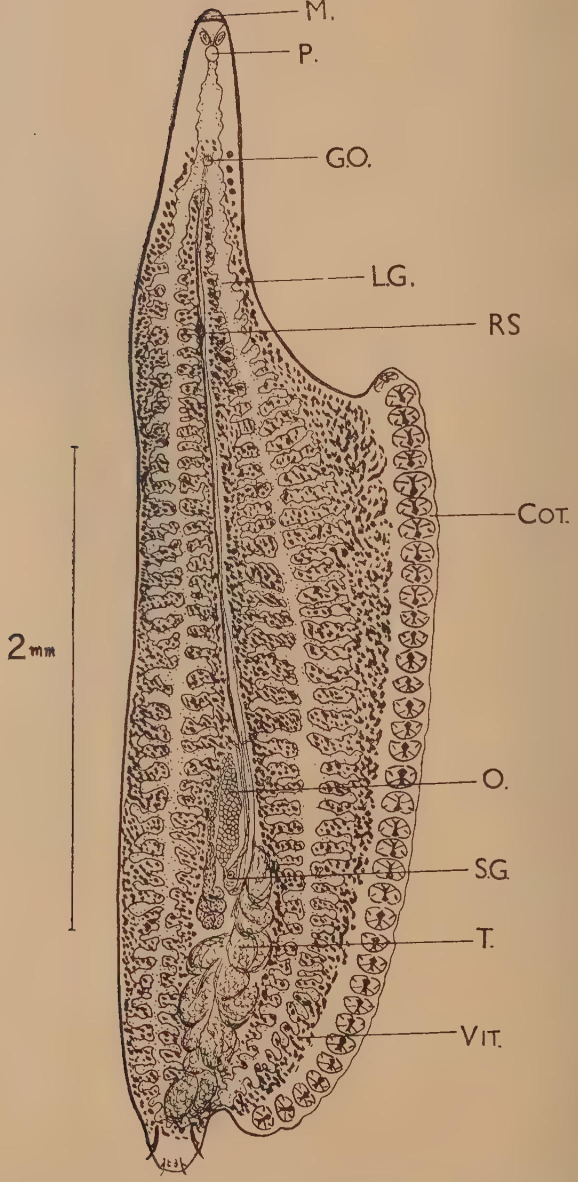
M.
P.
G.O.
L.G.
RS
COT.
2 mm
O.
S.G.
T.
VIT.

FIG. 1.—*Gastrocotyle trachuri*. Whole animal. Ventral view. COT.=cotylophore; G.O.=genital opening; L.G.=limb of gut; M.=mouth; O=ovary; P.=pharynx; R.S.=receptaculum seminis; S.G.=shell-gland; T.=testis; VIT.=vitellaria.

trematodes were seldom found and vice versa—a fact also noticed by W. H. Leigh-Sharpe (1933).

Gastrocotyle trachuri (Fig. 1) is an elongated worm 4·7 mm. long, narrow in its anterior third but considerably broader (1·2 mm.) in its posterior two-thirds along the left side of which is borne the cotylophore. The cotylophore bears one series of 32–40 suckers, each sucker measuring 0·08 mm. in diameter. Van Beneden and Hesse (1864) give the number of suckers as 31–38, and Paroni and Perugia (1890) as about 35. The armature of the suckers (Fig. 2, A) is very different from that described by van Beneden and Hesse. At the extreme posterior end of the body are 6 uncini, the lateral pair being large and stout and the two medial pairs small (Fig. 2, B).

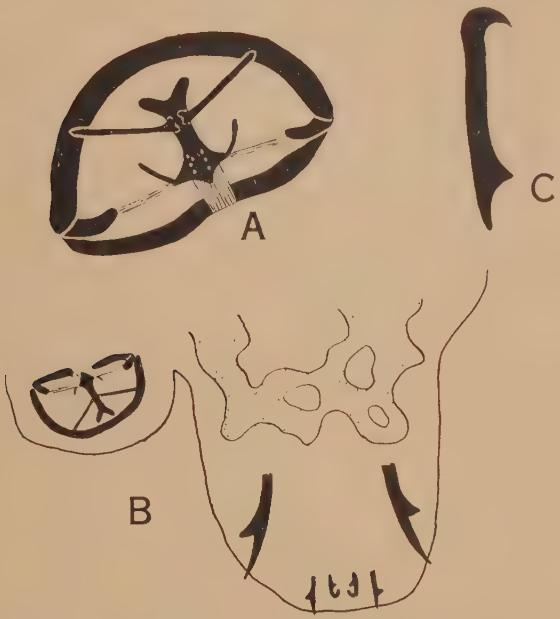

FIG. 2.—A. Armature of sucker; B. Posterior end of body; C. Crotchet from genital opening.

The Alimentary System. The mouth is terminal at the anterior end and leads into a buccal cavity in which are situated two lateral oval suckers measuring $23\mu \times 15\mu$. From the buccal cavity emerges the pharynx, measuring $46\mu \times 30\mu$, which leads into the œsophagus. The œsophagus is 0·2 mm. in length and has pouches in its walls but no actual diverticula. The gut extends down on either side of the body and has numerous diverticula and in the posterior end of the body the limbs of the gut anastomose (Figs. 1 and 2, B).

The Reproductive System (Fig. 3). The testes and ovary are situated in the posterior third of the body in the mid-line. The testes are situated more posteriorly and consist of closely apposed lobules. The vasa efferentia unite to form a fine vas deferens which passes in close apposition to the uterus up to the genital atrium into which it opens. The ovary is a ∩-shaped organ containing ripe ova in one extremity, from which emerges a short oviduct which leads into the shell-gland. From the shell-gland

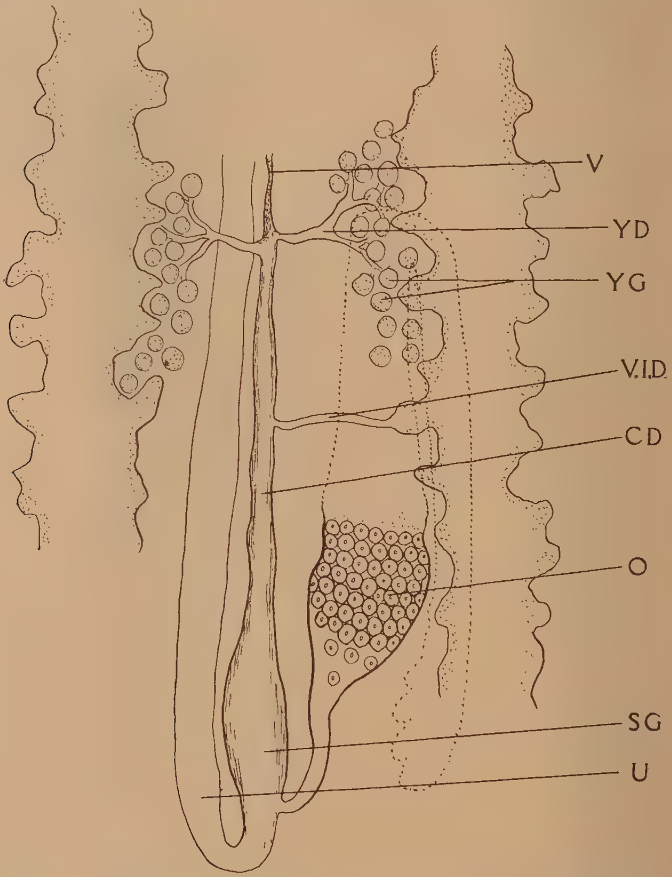

Fig. 3.—Shell-gland and associated structures. C.D.=connecting duct; O.=ovary (partially in outline); S.G.=shell-gland; U.=uterus; V.=vagina; V.I.D.=vitello-intestinal duct; Y.D.=yolk-duct; Y.G.=yolk-glands.

emerges the uterus which is a non-convoluted wide thin-walled tube leading up to the genital atrium into the base of which it opens (Fig. 4).

The genital atrium (Fig. 4) is a muscular sac 23μ in diameter, and at its apex is the genital opening which is situated in the mid-line ventrally, a short distance from the anterior end of the body. The opening is guarded by 12 crotchets arranged in a circle. Each crotchet (Fig. 2, C) has a bifurcate base and a hooked extremity, not a simple base and a flattened diamond-shaped extremity as described by Paroni and Perugia (1890, b).

The vagina opens in the mid-line on the dorsal surface a short distance behind the genital opening. It leads into a receptaculum seminis from which a duct emerges which proceeds downwards between the uterus and vas deferens and at the level of the upper border of the ovary receives the vitelline ducts on each side and then passes down into the shell-gland (Fig. 3), giving off the vitello-intestinal duct on the left.

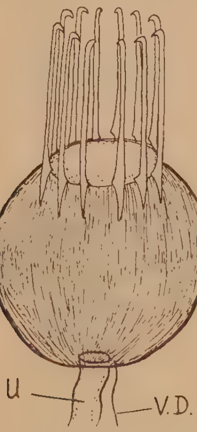

Fig. 4.—Genital atrium and opening. U.=uterus; V.D.=vas deferens.

The vitellaria are scattered diffuse lobules lying between the diverticula of the gut and a few lie anterior to the genital opening. None pass into the cotylophore.

The eggs are described by van Beneden and Hesse, and Paroni and Perugia as possessing two short filaments. No eggs were found in these specimens, so this fact cannot be confirmed.

I am indebted to my friend and former teacher, Mr. W. H. Leigh-Sharpe, for his help in finding these specimens.

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Rhopalura granosa sp. nov., an Orthonectid Parasite of a Lamellibranch *Heteranomia squamula* L., with a Note on its Swimming Behaviour.

By

D. Atkins, B.Sc.

With 4 Figures in the Text.

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INTRODUCTION.

THE Orthonectida, a small group of rare parasites, have attracted considerable interest owing to their doubtful systematic position. In 1868 Keferstein (1868, pl. ii, fig. 8) figured, though he did not describe, a "problematic parasite"* from the digestive tube of *Leptoplana tremellaris*, but it was not until about 1877 that a serious investigation of these forms was undertaken by Giard (1877), who gave to the group the name of Orthonectida. Our knowledge of the organisation and life-history of these parasites, however, is in great part due to the admirable researches of Caullery and his collaborators. The Orthonectida are forms in which the sexual generation is formed asexually from germ cells produced in a parasitic plasmodium.

Some eight species of Rhopalura, and one of Stœcharthrum, are now known.

Rhopalura granosa sp. nov., parasitic in *Heteranomia squamula* L. (=*Anomia aculeata* Müller), in the Plymouth area, is the first Orthonectid to be described from a Mollusc, members of the group being hitherto known from Annelids, Nemertines, a Planarian, and from an Ophiuroid, *Amphiura squamata*. The only previous record of an Orthonectid for the British Isles would seem to be that by McIntosh in 1873 (p. 129), when he described a curious parasite burrowing in the body wall of *Lineus gesserensis*. The specific name *granosa* has been given on account of the presence of characteristic refringent bodies in the male (see p. 237).

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* This species was named *Rhopalura* (*Intoshia*) *leptoplanæ* by Giard (1880, p. 236); it was rediscovered and described by Jourdain (1880)—under the name of *Prothelminthus hessi*—at Saint-Vaast-la-Hougue, and by Caullery and Mesnil (1901 c, pp. 399–400) in the bay of Saint-Martin, under the old fort of Saint-Germain-des-Vaux.

DESCRIPTION OF *RHOPALURA GRANOSA*.

In *R. granosa* the sexes are separate, and, as in other species of Rhopalura where the male is known, exhibit sexual dimorphism. Sexual dimorphism is so marked in the genus that Giard (1879, 1880) originally referred the two sexes in *R. ophiocomæ* to two genera, Rhopalura and Intoshia.

The Female.

The female (Fig. 1, A and B) is cylindrical, tapering anteriorly and posteriorly, and about 190 to 210μ long, and 60 to 75μ broad, not including the cilia. Individuals, however, vary somewhat in shape, doubtless partly owing to their considerable powers of contraction; a narrow elongated female, ca. 230μ long and 55μ broad, is shown in Fig. 1, B, but this is an extreme form, and rarely seen.

Fig. 1, A and B, of *R. granosa* recall Julin's figures of "femelle aplatie" and "femelle cylindrique" of *R. ophiocomæ* (Julin, 1882, pl. ii, figs. 2 and 1). The type of female shown in Fig. 1, A, is not flattened, however, for there is no appreciable difference observable in the width as it rotates in swimming; the rings are no less clearly marked than in the elongated form (Fig. 1, B). Both forms are found among those issuing naturally from their hosts. Caullery and Mesnil (1901 c, pp. 395–397) think that possibly the cylindrical females of *R. ophiocomæ* are a temporary state, leading to the flattened females: their specimens were apparently taken artificially from the host.

The body of the female *R. granosa*, which is entirely ciliated, shows eight rings, of which the first is the anterior, and the last the posterior terminal cone. The fourth and sixth rings seem to be formed of two rows of cells, while the second, third, fifth and seventh are formed of one row each. The anterior and posterior cones are formed of several rows. Between the rings there is a row of tiny cells, as in the male. The rings are superficial, involving the ectoderm only, the body not being segmented: they are more evident in some individuals than in others. When the animal is swimming forwards the cilia on the anterior cone are directed forwards, and those on the body posterior to it backwards (see Fig. 1, A). When the animal is swimming backwards, however, those on the second ring, as

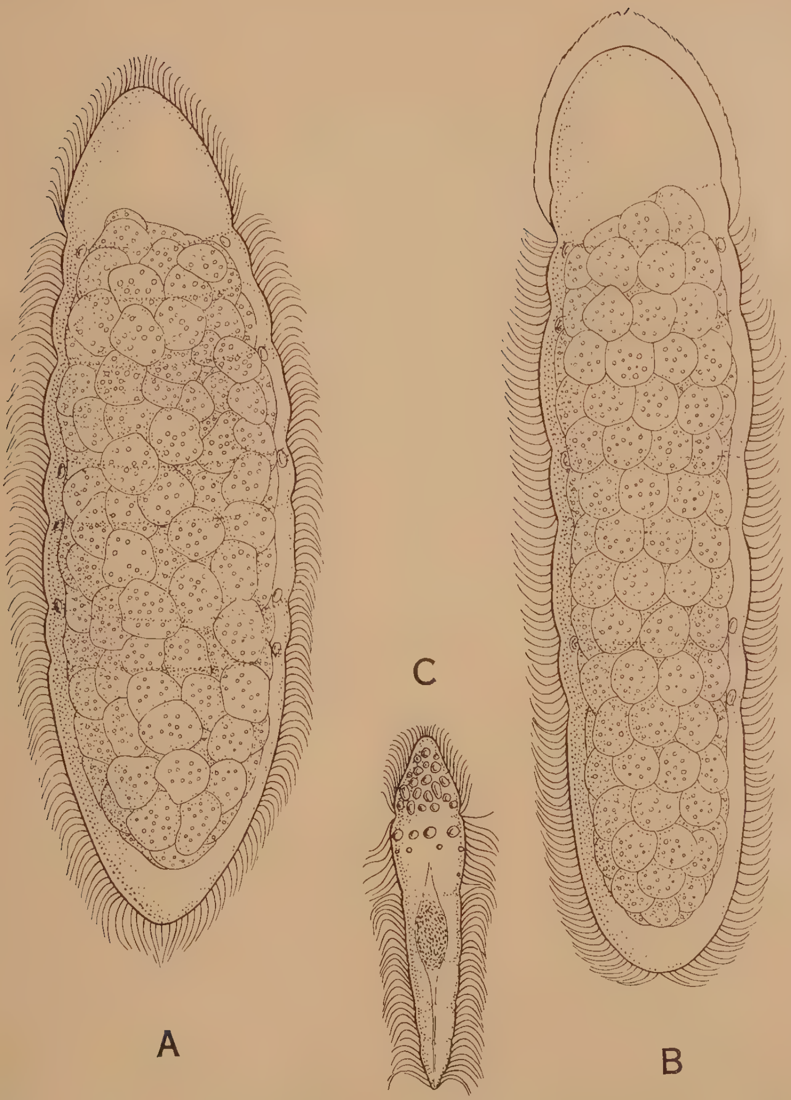

FIG. 1.—*Rhopalura granosa*. Sketches from life of individuals which had issued naturally from the host. The cilia are shown in profile only, although actually the animals are entirely ciliated: they are shown somewhat diagrammatically. × 573$\frac{1}{3}$.

A. Female. The cilia are shown as they appear during slow forward movement.

B. Rare, elongated form of the female. The cilia are shown as they appear during reversed swimming. In both forms the asymmetrical anterior extension of the mass of ova is due to the presence of the problematical organ, which is not shown in the figures.

C. Male.

well as those on the anterior cone, become motionless and are applied closely to the surface of the body, the tips being directed anteriorly (see Fig. 1, B, and also p. 247).

The ectoderm cells of the anterior and posterior extremities are deeper than those covering the rest of the body, the depth of the anterior cells being especially noticeable. The latter, in particular, contain a number of granules towards their outer ends, which become red if a trace of neutral red is added to the water. In sections of animals preserved in Bouin's fixative and stained with Heidenhain's iron hæmatoxylin and acid fuchsin the ectoderm cells appear much vacuolated, the vacuolation occurring sometimes at the inner ends, and sometimes at the outer ends of the cells. A problematical organ is present in the anterior cone; narrow prolongations from the organ appear to encircle the cone. It has been suggested by Metschnikoff (1881, p. 285) that this structure may be a remnant of an alimentary canal, and by Caullery and Lavallée (1908 b, p. 465) a nervous ring. A few, one to four, large vacuoles are generally observable in the cells of the anterior cone.

A small number of refringent bodies occur at irregular intervals, in a position between the rings of the body. These become orange with neutral red, and pale blue with methylene blue *intra vitam* staining.

The ova are numerous, very roughly about two hundred. They extend only slightly into the region of the anterior cone. They are about 14μ in diameter, with transparent cytoplasm containing a number of refringent granules, which become red with neutral red used *intra vitam*: it would appear to be these granules which in sections of material preserved in Bouin's fixative stain black with iron hæmatoxylin.

The embryos develop in the body of the parent: they are closely packed, and no movement of the ciliated larvæ is observable, such as occurs in *R. pelseneeri* (M. and C., 1905a, p. 429).

Embryos and ova have been observed, on several occasions, escaping from the parent in the region of the second and third rings. The fact that ova also have been seen to be expelled, points to the conclusion that these occurrences were not normal, but possibly due to unnatural conditions of observation; the position of emergence may, therefore, also be abnormal. A genital pore, such as described by Caullery and Mesnil (1901 c, p. 394) for *R. ophiocomæ*, could not be distinguished, at least in females sectioned while still within the host: no sections were made of those which had emerged.

The Male.

The male (Fig. 1, C) is cylindrical and slender, tapering anteriorly and posteriorly, the broadest region being the second ring. It is 87 to 95μ long and 20μ broad, not including the cilia. The body shows six superficial rings, of which the first is the anterior, and the last the posterior terminal cone. Between the rings is a row of tiny cells, the nuclei of which show clearly in sections. The anterior cone is formed of several rows of ectoderm cells, as is also the second ring.

A characteristic of the male is the presence of large irregular refringent bodies in the cells of the anterior cone, as well as in the first row of cells of the second ring. Occasionally smaller refringent bodies occur in other parts of the second ring. In *R. ophiocomæ*, the only other species in which the males are known to have these curious large refringent bodies in the cells, they are present in the second ring only (Giard, 1880, p. 229; Julin, 1882, p. 11). In sections of *R. granosa* preserved in Bouin's fixative these bodies frequently stain lightly with a dark periphery with iron hæmatoxylin and acid fuchsin, but others stain uniformly black. Caullery and Mesnil (1901 c, p. 393) found those of *R. ophiocomæ* disappeared in preparations treated with alcohol and xylol, a vacuole occupying their place. The fixative they used chiefly was a saturated solution of sublimate in sea-water, with the addition of 1% acetic acid.

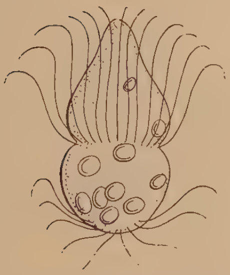

FIG. 2.—*Rhopalura granosa.* Ciliated larva, taken from the body of the parent. × 1470.

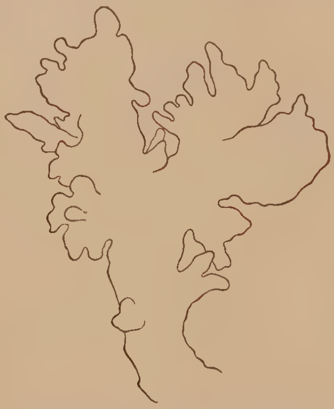

FIG. 3.—*Rhopalura granosa.* Fragment of a male producing plasmodium. × 70.

The male of *R. granosa* is entirely ciliated. The cilia on the anterior cone are rather shorter and denser than those on the rest of the body; they are directed forwards as in the female. Those on the second ring are much less closely set than those on the posterior rings, but appear to be as long. In *R. ophiocomæ*, the species which—of those so far described—seems most closely allied to *R. granosa*, the second ring is said to be unciliated, though Caullery and Mesnil (1901 c, p. 392 footnote) note that some isolated cells exceptionally bear long cilia. In sections the basal granules of the cilia stain very darkly and clearly with iron hæmatoxylin.

The "testis" is present about the middle of the body. The spermatozoa are flagellated.

The Larva.

The ciliated larva (Fig. 2) forced from the body of the female, by gentle pressure on the coverslip, is somewhat acorn-shaped,* being slightly constricted in the middle region, pointed anteriorly and broadly rounded posteriorly. (The pointed end is apparently anterior, as this is foremost when the larva swims.) It is about 19μ long. Ciliation is restricted to two bands of long cilia; one in the middle region about the slight constriction, and one posteriorly. Refringent bodies are present in both regions of the larva, but chiefly posteriorly. Cells could not be distinguished in the living state; larvæ were not sectioned.

The larva of *R. granosa* differs considerably in appearance from those so far described, namely, that of *R. ophiocomæ* (C. and L., 1905, p. 266; 1908 b, p. 432, and pl. xv, figs. 43, 44) and *R. pelseneeri* (M. and C., 1905 a, p. 429, and fig. 1), which appear to have no regular arrangement of the cilia, though Caullery and Lavallée (1908 b, p. 432), speaking of the very small size (12–15μ in diameter) and great transparency of the former larva, say: "La disposition des cils mêmes est à peu près impossible à fixer; ils paraissent longs et peu denses. Ils donnent à ces larves un mouvement rapide, souvent tourbillonnant."

Relationships.

Caullery and Mesnil (1901 c, p. 419) have distinguished three groups in the genus Rhopalura, characterised as follows:—

Cilia limited to narrow rings, *R. pterocirri* St. J. (I).

Cilia entirely (or nearly) covering the body.	Ova in compact mass. (II).	*R. ophiocomæ* Gd. *R. intoshi* Metchn.
	1 (or 2) linear row of ova. (III)	*R. leptoplanæ* Gd. *R. pelseneeri* C. and M. *R. linei* Gd. *R. metchnikovi* C. and M. *R. julini* C. and M.

R. granosa evidently belongs to the second group. It is intermediate in size in both sexes, between *R. intoshi* from *Lineus* (*Nemertes*) *lacteus* and *R. ophiocomæ* from *Amphiura squamata*. In the male it is clearly distinguishable from *R. intoshi* by the presence of large refringent bodies, and from *R. ophiocomæ* by having these bodies in the anterior cone, and the first row of cells of the second ring, while in *R. ophiocomæ* they are restricted to the second ring.

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* Shaped like an acorn in its cup.

The female of *R. granosa* has not been observed to be without cilia on the second ring, as occurs in certain individuals of *R. ophiocomæ* (Giard, 1880, p. 232; Julin, 1882, p. 16; C. and M., 1901 c, p. 393): it has eight rings, while that of *R. intoshi* has nine (Metschnikoff, 1881, p. 284).

The larva differs from that of *R. ophiocomæ* both in the shape and the arrangement of the cilia: the larva of *R. intoshi* is unknown.

The Plasmodia and their Distribution in the Host.

In *Heteranomia squamula* the parasite is found replacing the gonad; it also occurs in the blood lacunæ and vessels in the mantle and the suspensory membranes of the gills, even extending into the dorsal ends of the gill filaments. In one host sectioned, numerous young plasmodia were present in the mantle margin in the posterior region. In heavy infections the parasitic plasmodia, containing the sexual forms of the Orthonectid, entirely replace the gonad of the host, rendering the determination of sex impossible. A fragment of a male containing plasmodium is shown in Fig. 3.

It would appear to be more usual for the males and females to occur in separate hosts, though it is by no means rare for them to be found together (see p. 244); when this occurs one sex generally predominates. Observations were mostly made on living Heteranomia, only two specimens being sectioned. One of the sectioned individuals was parasitised by plasmodia containing males only, many of them being nearly mature. It was well infected, plasmodia occurring in the mantle, visceral mass, suspensory membranes of the gills and dorsal ends of the gill filaments, but much of the gonad remained, sperm being recognisable among degenerating cells in some regions.

The second Heteranomia sectioned was very heavily infected, no gonad being recognisable. The great majority of the plasmodia in this host contained female Rhopalura, but in four separate regions of the visceral mass and mantle, males were present, many being nearly mature, and in at least two of these regions males and females occurred together in the same plasmodium (see Fig. 4). In one region (a), several branches or lobes of a plasmodium contained males, but in a very small portion only were the two sexes present together. In a second region (b), a small island of well-formed males, together with numerous germ cells and groups of germ cells, was present among females, and the males were not segregated in separate lobes of the plasmodium. In a third region (c), a few males were present in a small, almost empty plasmodial lobe, which was rather doubtfully traced into a female plasmodium. The fourth region (d), near the byssal muscle of the host, was by far the largest. This plasmodium appeared to contain males alone, though its considerable size made the tracing of its many branches difficult.

Where the males and females were present in the same plasmodium, the females yet appeared to contain unsegmented ova, so far as could be ascertained in the crowded condition of these. Caullery and Mesnil (1901 c, pp. 466–467) state that " dans des coupes d'une Amphiura, *qui renfermait des plasmodes des deux sexes* (of *R. ophiocomæ*), plusieurs femelles, à l'intérieur desquelles, au lieu d'ovules, on trouvait des corps plurinucléés ayant tout à fait l'aspect des embryons décrits ci-dessus, mais un peu moins avancés. Nous les interprétons comme tels. Il est parfaitement admissible que, lorsque les deux sexes de Rhopalura existent dans une même Ophiure, les femelles adultes puissent, avant d'arriver au dehors, être fécondées et renfermer des embryons."

It is impossible to be entirely certain that the presence of males and females in the same plasmodium is not due to the disappearance of host tissue dividing two originally separate plasmodia, but it seems not improbable that a plasmodium may produce males and females at different times, the two phases overlapping to some extent. When plasmodia are well established in the host, they ramify greatly, and it is practically impossible to determine their number and limits. The presence of plasmodia with males only in the less heavily infected host sectioned would seem to indicate that, if it should prove to be correct that the two sexes are produced by the same plasmodium at different times, the male phase precedes the female.

It may be noted that curious thread- or rod-like bodies, or regions, of darker staining protoplasm were present in some small portions of female producing plasmodia. Among masses of these occurred a few normal-looking groups of germ cells. The significance of these bodies is obscure ; they may be a normal occurrence, or possibly parasites.

Caullery and Mesnil (1901 c, p. 384 ; C. and L., 1912, p. 159) have described plasmodia which produce one sex only, such as are usually found in *R. ophiocomæ* from *Amphiura squamata*, as " unisexual," and those in which males and females develop side by side in the same plasmodium, as in *R. metchnikovi* from *Spio martinensis* (C. and M., 1901 c, pp. 384, 402), as " hermaphrodite." In *R. intoshi* from *Lineus* (*Nemertes*) *lacteus* an intermediate condition, between that of *R. ophiocomæ* and *R. metchnikovi*, seems to obtain, " male," " female," and " hermaphrodite " plasmodia frequently occurring in the same host (Metschnikoff, 1881, p. 284).

Most known diœcious species of Rhopalura apparently have " hermaphrodite " plasmodia (*R. leptoplanæ*, C. and M., 1901 c, p. 399, and *R. julini*, C. and M., 1901 c, p. 412, in addition to those already mentioned), *R. ophiocomæ* being the only one with generally " unisexual " plasmodia.

There appears, however, to be considerable variation in the condition of the plasmodia of this species in different localities. Giard (1880, p. 228) and Metschnikoff, 1881, p. 288) found that in *R. ophiocomæ* from *Amphiura squamata* from Wimereux, and from Naples and Spezzia respectively, a plasmodium produced Orthonectids of one sex only, males or females, though very occasionally the two sexes might be present in the same host. Julin (1882, p. 8), also working at Wimereux, says: "Je n'ai jamais rencontré dans le même hôte que l'une des deux formes, soit le mâle, soit la

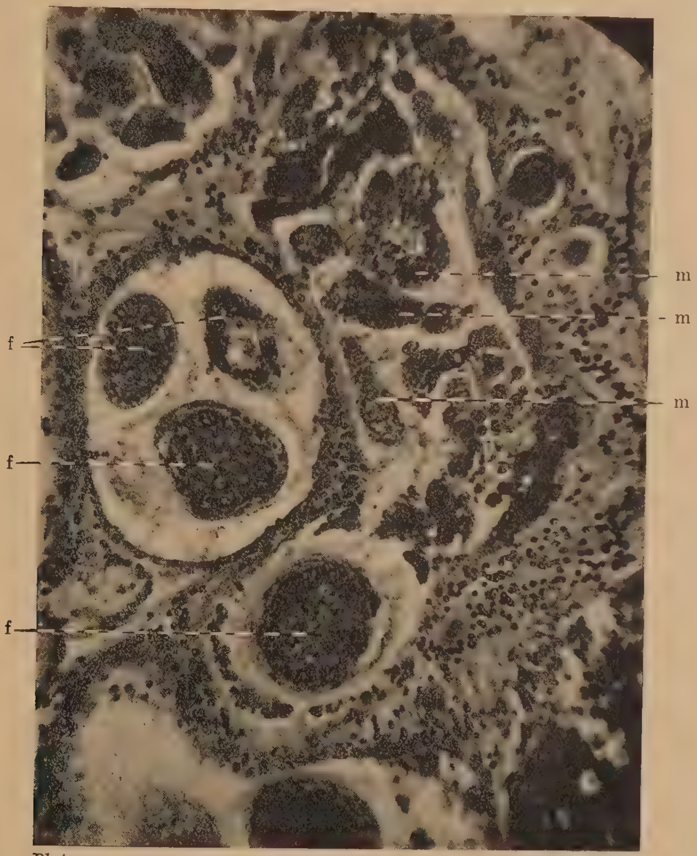

Photo. *D. P. Wilson.*

FIG. 4.—*Rhopalura granosa.* Section of part of a plasmodium containing both males and females. F., female (transverse section); m., male (longitudinal section). Bouin's fixative: Heidenhain's iron hæmatoxylin and acid fuchsin. × ca. 1012.

femelle, . . ." Caullery and Mesnil (1901 c, p. 392) found "Dans le cas de la *Rh. ophiocomæ*, chaque plasmode ne renferme que des individus d'un seul sexe, et souvent dans une même Ophiure, tous les plasmodes sont du même sexe," and in a foot-note add : "Dans l'anse Saint-Martin, un tiers environ des Ophiures parasitées renfermait uniquement des femelles, un tiers uniquement des mâles, un tiers à la fois des mâles et des femelles." On the other hand Koehler (1886, p. 609) working at Cette on the same species very frequently found males and females in the same Amphiura, the latter always being less numerous than the males. He rarely found one sex only ; in some fifty infected Ophiuroids only two contained males alone. He not only found males and females in the same host, but in the same plasmodium. Working in the same months of the year as Julin, he says (1886, p. 610) that the difference in their results can hardly be due to season, but that "Le genre de vie de ces remarquables parasites n'est donc pas le même à Cette qu'à Vimereux." In 1901 Caullery and Mesnil (p. 392) record that in an exceptional case they found adult males and females, together with developmental stages of both sexes, in the same plasmodium of *R. ophiocomæ*, thus confirming Koehler's observation of 1886.

In *R. ophiocomæ*, where the host is parasitised generally by Orthonectids of a single sex (with the exception of Amphiura at Cette), Caullery and Lavallée (1912, p. 163, foot-note) believe that the infection has mostly arisen from a single larva, and that the rare instances where males and females are present in the same host, have arisen from multiple infection by larvæ of different sexes. They think that one larva may possibly give rise to several amœboid germs, which spread the infection in the host (1912, p. 153).

When mature the males and females leave the host. Those from the gonad of Heteranomia would seem to pass out by way of the renal ducts, for in sections free forms have been recognised in them. The renal ducts opening into the exhalent chamber, the parasite will pass out safely in the exhalent current of the host. The way of escape of those parasites present in the blood-vessels and spaces has not been observed.

The males and females apparently meet outside the host and fertilisation is effected. The mode of fertilisation was not observed in *R. granosa*. It has, however, been studied in *R. ophiocomæ* by Caullery and Lavallée (1908 b, pp. 428–430). They found that on mixing mature males and females artificially taken from the host, "Au bout de 10 à 15 minutes, on observe *très fréquemment* que des mâles sont remorqués, aux flancs des femelles, dans la moitié postérieure de celles-ci, comme s'ils s'étaient accidentellement pris dans le revêtement ciliaire et n'avaient pu s'en dégager. Une femelle remorque parfois deux mâles ; nous en avons même observé, une fois, trois.

Ce phénomène, extrêmement commun dans les premiers temps du mélange, ne se retrouve plus ensuite. Nous avons pu nous convaincre que ces rencontres des mâles et des femelles étaient les circonstances mêmes de la fécondation. Et cependant, la façon dont nagent les deux catégories d'individus n'indique nullement qu'ils se recherchent. On voit les mâles passer très près des femelles sans a'y fixer. Il semble que ce soit purement le hasard qui produise les couples observés. Le contact des deux sexes n'est d'ailleurs jamais très long. Au bout de quelques minutes, les mâles se sont dégagés, les femelles sont de nouveau solitaires. Ce contact n'est jamais non plus intime. Le mâle paraît simplement retenu par sa ciliation à celle de la femelle.

. . . nous avons constaté, d'une façon indiscutable, que les spermatozoïdes sont émis, à ce moment, au dehors. . . .

Caullery et Mesnil (1901, p. 394, pl. x, fig. 2, og.) ont signalé, sur la surface de la femelle, un pore, appelé par eux *pore génital* ; . . . Nous avons lieu de croire que c'est par là que les spermatozoïdes pénètrent."

The embryos develop while in the body of the parent, being liberated as ciliated larvæ. To Caullery and his collaborators is due the discovery that in the Orthonectida the ciliated larvæ carry infection to fresh hosts ; Caullery and Lavallée (1910, 1912) have caused experimental infection of *Amphiura squamata* by *R. ophiocomæ*.

They (C. and L., 1912, p. 140) have discovered that in the life-history of the Orthonectida two generations alternate regularly :—

(1) a sexual generation, constituted in most species of males and females (some species, e.g. *R. pelseneeri*, are hermaphrodite) formed asexually from germ cells produced in the parasitic plasmodium.

(2) a generation produced from the fertilised ova of the preceding generation and carrying infection in the larval state to new hosts, where these larvæ are transformed into plasmodia, which give birth to the sexual generation.

It is puzzling to imagine how minute ciliated larvæ can effect safe settlement in a Lamellibranch. In the Anomiidæ the action of the lateral cilia on the gills is particularly furious, and the inhalent current rapid. One would not expect larvæ of not more than 19μ in length to be sufficiently strong swimmers to resist such a current, though it is possible that their cilia may interlock with those on the gills. If carried to the dorsal groove between the two demibranchs of each side they would in all probability eventually reach the mouth. It is possible, however, that after being thrown against the gills, they may be carried to the free edges of these, and then posteriorly in the rejection current, and dropped on the mantle margin in the posterior region. It may be noted that in one of the two Heteranomia sectioned, numerous young plasmodia were found in the mantle margin in this region, but the actual path of infection remains obscure.

If a number of Heteranomia from an infected batch be placed in a finger-bowl, numerous specimens of *R. granosa* may be obtained after a time. These will live quite happily in sea-water, whereas those obtained by opening the hosts, being not yet fully mature and ready for their free life, very quickly die. Even the cilia of immature forms frequently break down into droplets. It is remarkable that males, sufficiently mature for the sperm to be active, yet, when artificially liberated from the host die after a very few minutes in sea-water. In well-formed males obtained in this way sperm is frequently seen issuing from about the middle of the body (see also Julin, 1882, pp. 13–14), but this is almost certainly abnormal and not the true method of emission.

If a jet of air be passed through the bowl, the Heteranomia will live for weeks, and a supply of Rhopalura be available. A number of Heteranomia have been kept in this way for some fourteen weeks, though towards the end of that time specimens of Rhopalura were difficult to find, and females with segmented ova rare.

R. ophiocomæ issues from *Amphiura squamata* chiefly in the late afternoon ; Caullery and Lavallée (1912, p. 143) suggest that the more or less fixed hour of emergence, providing for the simultaneous emission of the males and females, brings about the meeting of the sexes. No observations were made on the time of emergence of the Orthonectids from Heteranomia.

NUMBER AND DISTRIBUTION OF THE HOSTS INFECTED.

The infected Heteranomia, with one exception, have been obtained from masses of *Lepralia foliacea*. The Rhopalura was first found on November 25, 1932, infecting Heteranomia taken from a mass of Lepralia turned out of the Plymouth Aquarium, but which had most probably come from off Revelstoke Point or Stoke Point. Ten out of twenty-two (45·4%) of the Lamellibranchs were found to be infected. Of these seven were infected with plasmodia containing females, and three with plasmodia containing males. In an unnoted number of Heteranomia infected with female forms, males were also present. This high percentage of infection, which has so far not been reached in material examined direct from the grounds, may possibly have been artificially induced by favourable conditions in the tanks.

On February 2, 1933, 149 Heteranomia from fragments of Lepralia dredged from off Revelstoke Point were examined. Of these twenty-four (16·1%) were found to be infected ; ten with males, ten with females (in one the plasmodia contained only immature forms, which from their size were probably female), and four with both males and females. When both sexes were present together the males were the more numerous, but as they are so much smaller than the females it does not necessarily follow that the plasmodia producing males occupied more space in the host than those producing females. The hosts varied from 3 to 10 mm. in diameter: that of 3 mm. was parasitised by male-bearing plasmodia.

The following animals, living either attached to, or sheltering in the crevices of the Lepralia obtained on February 2, were examined, but unsuccessfully, for the presence of Orthonectids: ten *Chlamys distorta*, ten *Ophiothrix fragilis*, five *Ophiocomina nigra*, and one *Antedon bifida*.

On February 6, 1933, 165 Heteranomia from fragments of Lepralia trawled from off Revelstoke and Stoke Points were examined. Of these only eleven (6·6%) were infected; four with males, five with females, and two with both males and females. In four the infection was slight. The hosts varied from about 6 to 12 mm. in diameter.

On February 13, 1933, all the Heteranomia of any size from three large pieces of Lepralia trawled from off Stoke Point were examined. Of the ninety obtained fourteen (15·5%) were infected; nine with males, two with females, and three with both males and females. Where the two sexes were present together the males were much more numerous than the females. The hosts varied from about 5 to 14 mm. in diameter.

The Heteranomia obtained on February 2, 6, and 13 were opened and carefully examined at a magnification of about 140, so that it is unlikely that even small numbers of well-developed sexual forms would have been overlooked, though tiny plasmodia most probably would have been.

Thirty-eight Heteranomia from twenty-four *Chlamys opercularis* from the "Corner" Ground off the Mewstone were examined on January 20, 1933: none were found to be infected.

An examination of seventy-three Heteranomia taken from the carapace of a single *Maia squinado* from the Mewstone Ground on March 20, 1933, showed only one to be infected, and that with plasmodia containing males alone.

It is possible that only those Heteranomia which occur in large communities, such as on masses of Lepralia, will be found to be generally infected. The branching colonies of the Polyzoan would also provide shelter from dispersing currents for the Orthonectids emerging from their hosts, thus facilitating the meeting of the males and females. Colonies of *Lepralia foliacea* were dredged and trawled chiefly off Revelstoke and Stoke Points at a depth of from 15 to 22 fathoms.

R. ophiocomæ, a species on which most work has been done, has been found to infect 2·5% to under 10% of *Amphiura squamata* (Giard, 1880, p. 227; Julin, 1882, p . 9; Caullery and Lavallée, 1908 b, p. 425), varying widely in different parts of the same locality (Caullery and Mesnil, 1901 c,

p. 391; Koehler, 1886, p. 609), and in different years (Metschnikoff, 1881, pp. 287, 288).

The Swimming Behaviour of *Rhopalura granosa*.

The Orthonectida were so named by Giard from their habit of swimming in a straight line. Giard states (1877, translated 1878, p. 182): "By the name of Orthonectida I have desired to recall their progression, which is so characteristic that it would of itself suffice for their recognition among the parasites with which they might be confounded."

In *R. granosa* this habit would seem to be very generally confined to animals travelling relatively slowly, as they frequently do on being artificially liberated from the host. It was apparently on individuals of *R. ophiocomæ* and *R. linei* obtained in this way that Giard made his observations. Observations on *R. granosa* have been made on individuals which had issued naturally from the hosts; mostly on females because of their larger size. The males swim more rapidly than the females, for although there is little difference in the length of the cilia in the two sexes, the males are less than half the size of the females.

The females, when normally active, continually take short flights upwards, often touching the bottom of the watch-glass or finger-bowl only to leave it almost immediately: the males less frequently touch the bottom. They turn in all directions, this apparently being due to bending of the body. It is only when their activity becomes much reduced that they travel largely in contact with the substratum, and then nearly always in a straight line. When swimming at speed these Orthonectids mostly, though not invariably, follow a gently spiral path. They may, on occasion, swim almost perpendicularly upwards, and on reaching the surface film (in a watch-glass of water) swim beneath it for a short distance, before diving downwards again. It is particularly when an animal is swimming perpendicularly upwards that it may be observed to follow a spiral path, for the anterior end of the animal is seen to describe tiny circles. *R. granosa* is symmetrical, with apparently no longitudinal differentiation of cilia, but any slight bending of the body out of a straight line—such as might well occur in an animal capable of muscular contraction—would, owing to the rotation of the animal on its own axis, result in a spiral path being followed.

The cilia on the body do not beat directly backwards, but obliquely, and the animal moves forwards, rotating on its own axis to the left. This is actual, and not apparent rotation due to the appearance of metachronal waves. During backwards swimming the animal rotates to the right.

Caullery and Mesnil (1901 c, p. 402) noted that the males of *R. metchnikovi* while in the plasmodia "montrent une assez grande mobilité; ils tournent sur leur grand axe à la façon d'une toupie." It is also of interest that they remark of the male, which is globular, measuring 40μ by 30μ, with the anterior extremity larger than the posterior, "En raison sans doute de sa forme globuleuse, il n'a pas le mouvement en ligne droite, si général dans le groupe et que nous avons constaté, en particulier, pour la femelle. Il est extrêmement mobile et il décrit des sortes de cercles ; il ressemble beaucoup à un Infusoire holotriche." It should be noted that Caullery and his collaborators—in common with previous investigators—in most of their work prior to that recorded in the 1912 paper, apparently used material obtained by opening the hosts.

As in other species of Rhopalura, there is in both sexes clear differentiation of the ciliation of the anterior cone from that of the rest of the body, in that when the animal is swimming forwards the cilia on the anterior cone appear to be directed forwards, while those on the rings posterior to it appear to be directed backwards (see Fig. 1, A). Over both regions, however, the effective beat is backwards, in spite of the difference in appearance. The appearance of the cilia on the anterior cone may be due to a restricted amplitude of beat ; when an animal is swimming slowly and the beat can be seen, they then certainly appear to beat through a small angle. That the effective beat is backwards over the anterior cone may be observed by the movement of particles caused by the action of these cilia in animals artificially liberated before maturity from their host, and in consequence have lost the rest of the cilia while in sea-water (see p. 244). It is of interest that the cilia on the anterior cone resist disintegration considerably longer than those on the rest of the body, and may frequently be seen intact and active, when the others have been shed. These cilia beating alone appear unable to move the animal. It is possible that they have a sensory function in addition to a locomotory one ; their differentiation from those on the rest of the body suggests this.

When the Orthonectids are swimming slowly forwards the appearance of the cilia is as shown in Fig. 1, A and C.

The cilia on the anterior cone, and in addition those on the second ring—though the latter during activity appear to be directed posteriorly with the cilia on the posterior rings—can be suddenly applied so closely to the surface that even at a magnification of 500 they appear as a thick, and but slightly striated cuticle (Fig. 1, B) ; during reversed swimming they were observed always to be motionless. In animals swimming forwards very slowly the cilia on the anterior cone have been observed, on occasions, to be motionless, but it is doubtful whether this occurs under normal conditions.

The cilia on the body posterior to the second ring rarely, if ever, become motionless, but the rate of beat may be much reduced temporarily so that the animal remains almost stationary. Females have been observed to remain for a time practically stationary, but with the body rotating.

This is apparently due to change of direction of beat of the cilia. They have also been seen to stand on end and rotate, being evidently attached posteriorly owing to some viscid property of the cilia in that region.

From observations it seems that the direction of beat of the cilia may be changed, for the Orthonectids are capable of swimming forwards and backwards, though the forward movement is the more usual. Frequently, however, females artificially liberated from their host may continue swimming backwards for the few minutes they live. McIntosh (1873, p. 129), one of the first observers of an Orthonectid, noticed the backward swimming of the parasite he found in *Lineus gesserensis.*

The change in direction of movement from forward to backward swimming is abrupt, the animal giving a sudden dart backwards as the cilia on the anterior cone and second ring are closed down ; during backward swimming these cilia have never been observed to beat, and would, therefore, seem to be incapable of reversing the direction of their beat.

In reversed swimming the cilia posterior to the second ring appear to be directed forwards (see Fig. 1, B)—that is in the opposite direction to that obtaining when the animals are swimming forward. Although it has been impossible to make observations on the movement of individual cilia, the change in direction of swimming would seem to be due to reversal of the effective beat of the cilia.

This power of sudden reversal of direction of movement is probably of value to the animal in rapid retreat from danger. On running into an obstacle, they have been observed frequently to swim in the reversed manner for a certain distance, then to turn round by muscular action, and continue the retreat in the same direction, but with the anterior end foremost. This reaction, however, does not invariably occur, for females at least appear to have a tendency to collect round debris, with the anterior end pushed against it, and the body cilia beating, though not at full speed. They frequently rub backwards and forwards against debris, at the same time contracting and expanding the body, and if the posterior extremity should come in contact, they have been observed to become caught—apparently by some viscid secretion or thread—and unable to free themselves, though the cilia, including those on the anterior cone, beat rapidly. The production of this viscid thread may perhaps be abnormal, due to the unnatural conditions of observation ; a female on one occasion was seen towing a male by such a thread, though at some considerable distance, and on other occasions females have been seen attached to each other posteriorly by a thread and tugging against each other, and so held stationary. It is just possible, however, that the viscid property of the cilia may play some part in the pairing of the males and females.

Males may frequently be observed continually reversing the direction of swimming, at very short intervals of time (a second or less). A characteristic movement of the male is that of sharply striking the water with the slender posterior region of the body: it is to this that the name Rhopalura refers (see Giard, 1880, p. 231).

I wish to thank the British Association for granting me the use of their table at Plymouth, and the Director and Council of the Marine Biological Association for facilities. For the microphotograph (Fig. 4) I am indebted to Mr. D. P. Wilson.

SUMMARY.

A new species of Orthonectid, *Rhopalura granosa* from *Heteranomia squamula* L., is described. The female is fusiform, and about 190 to 230μ long, and 55 to 75μ broad. The male is also fusiform, but less than half the size of the female, being only 87 to 95μ long and 20μ broad. *R. granosa* is distinguished from all other known species of Rhopalura by the presence in the male of large refringent bodies in the anterior cone, and in the first row of cells of the second ring. The male of *R. ophiocomæ* Giard, a species closely allied to *R. granosa*, has the refringent bodies in the cells of the second ring only.

The infected Heteranomia have been obtained from *Lepralia foliacea* trawled and dredged from off Revelstoke and Stoke Points. In Heteranomia examined direct from the grounds the infection in February, 1933, varied from about 6·6% to 16%, but in a number taken from Lepralia from the Plymouth Aquarium in November, 1932, the percentage of infection was as high as 45·4%.

The parasite is found replacing the gonad of the host; it also occurs in the blood lacunæ and vessels in the mantle, and in the suspensory membranes of the gills, even extending into the dorsal ends of the filaments. In heavy infections the Orthonectid may entirely replace the gonad of the host.

Male and female containing plasmodia usually occur in separate hosts, but it is not uncommon for the two sexes to be found together. From sections it would seem that males and females may on occasion be produced in the same plasmodium.

The swimming behaviour of *R. granosa* is described.

APPENDIX.

OTHER ORGANISMS OBSERVED IN *Heteranomia squamula*.

Few parasites and commensals, other than Rhopalura, were noticed in some four to five hundred Heteranomia examined. Those seen were :—

(1) Rounded masses, *ca.* 60 to 80μ in diameter, of tiny spores in the gonad of two individuals.

(2) A Coccidian in the kidney. The number of Heteranomia infected with this parasite was not noted.

(3) A Rhabdocœle from each of six individuals of the seventy-three taken from the carapace of a single Maia (see p. 245). This Rhabdocœle almost certainly was not *Graffilla gemellipara* Linton, which is common in the mantle cavity and in the gut of *Cardium edule* from the Yealm Estuary and Millbrook. Although the specimens were large they did not contain viviparous young as is characteristic of *G. gemellipara*, and were more opaque than that species: they were broadly rounded anteriorly and pointed posteriorly. In addition to these six specimens another two or three have been seen at different times.

(4) A few larval Trematodes were seen in two or three Heteranomia taken from the Maia mentioned previously.

(5) In a number of Heteranomia a ciliate, possibly a species of Boveria, was present on the mantle.

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On the Rate of Diatom Growth.

By

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With 3 Figures in the Text.

THE series of events taking place in the sea which influence the growth of phytoplankton, and consequently the general fertility, has provided a fruitful study during recent years. Intensive surveys have been made since simple and sufficiently accurate methods of determining minute traces of phosphates and nitrates in sea-water became available. Over the greater part of the oceans the annual crop of phytoplankton seems to be limited by the quantity of these nutrient salts which arrive annually in the upper layers from below. This quantity depends upon vertical mixing, since nitrogen salts and phosphates are re-formed but slowly from dead organisms, which sink meanwhile to enrich the deep layers. Although this hypothesis gives a simple explanation why some areas are fertile, supporting a rich growth of phytoplankton and others not so much so, and the facts so far ascertained fit well with the explanation, recent investigations in the Southern Ocean (**1**, **2**) indicate that other causes limit the annual production there. The phosphates and nitrates are not fully utilised during the summer, whereas in equally high and higher latitudes in the North Atlantic they are, and, moreover, growth may be very rapid.

A wealth of observations has been collected in widely distant seas, and the questions, often rather nebulous, which have arisen from these require consideration in any attempt to envisage the skein of possible factors which regulate the growth of diatoms in various places.

Purely mechanical means by which phytoplankton organisms are transported vertically may play a leading rôle. Off the west coast of Norway (**3**a, **4**) it has been found that the spring outburst of diatom growth starts around the edges of the fiords and over the edge of the continental shelf, then extending across the 30 miles of sea between these foci; later it commences in the Atlantic water beyond. In the Gulf of Maine (**5**) the spring outburst starts close inshore and over the offshore banks. Between Russia and the Northern ice (**6**) growth starts first inshore and in the cold Arctic water which has originated from comparatively shallow areas, later in the tongues of warmer Atlantic water which penetrate eastward into the Arctic water. It has been suggested that water near the surface close inshore and over banks where there is upwelling is better seeded with diatoms and their spores, these having been kept better in suspension throughout the winter by turbulence than in the deep ocean. Another likely locus (**3**b) where the surface layers are well seeded at the beginning of sunny weather is close to ice, where the run off remains near the surface and may often contain diatoms which have been frozen in at the end of the previous summer.

Vertical transport in the turbulent water of the open ocean is of necessity greater in those regions where wave motion keeps the water so well mixed that the upper layers do not gain in temperature over the water below. The continuous drain on the phytoplankton population by being carried below the "compensation level," where there is sufficient light for photosynthesis to exceed respiration, is enhanced in such areas, where vertical mixing is not restrained during the summer months owing to density differences being set up (**3**). Further, the surface waters being kept cold, the rate of photosynthesis is kept low. This may to some extent influence the fertility over wide and turbulent expanses of the Southern Ocean, where owing to the great "fetch" of the waves their mixing effect may extend deeper than in the North Atlantic.

It has recently been found in the seas between Iceland and Greenland (**7**), in the Barents Sea (**8**), and in the English Channel (**9**) that ammonium salts occur at greater concentration in the upper layers than in the deeper water. Although the quantity is always very small, some material amount remains after all or practically all the nitrate has been used up by phytoplankton. Nitrate production, which presumably takes place only by bacterial action, has not yet been found to occur in the upper layers of ocean water, although it occurs readily enough in water in contact with bottom deposits. It is not clear how the plants get a sufficiency of nitrogen salts during the summer months, at least in such places as the upper layers of the English Channel, unless they utilise ammonium as it is being formed. In fact, the numerous and more accurate data now accumulated have added little to our knowledge of the processes involved in the nitrogen cycle in the seas.

Physical conditions may explain, either wholly or in part, a group of phenomena connected with the growth of diatoms in temperate and Northern seas. The date of the vernal outburst of growth in the English Channel and off the Isle of Man has been found to depend largely on the amount of sunshine in the early part of the year, yet in Loch Fyne it may occur a month earlier than in the near-by Loch Striven (**10**). Off the west coast of Norway, in materially higher latitude and colder water, it occurs earlier than in the English Channel. The date may depend upon the total amount of incident light, of which there are no observations yet available, or upon some other cause not yet recognised.

In general it appears that the growth of diatoms during the summer months in relatively shallow inshore waters is greater than in deeper waters out to sea. Although the amounts of nutrient salts at the beginning of the season may not be very different, in the shallower areas mixing due to tides and occasional strong winds keep the upper water layer better refreshed with these salts throughout the summer. In this connection Gran (**3**) has put forward the interesting theory that drainage from the land contains some growth-promoting factor, which would in part account for the great productivity of coastal waters, and perhaps for the inability of phytoplankton to consume all the available nutrient salts in the Southern Ocean which receives little land drainage compared with the Northern Atlantic. It had been found that the addition of a sterilised water extract of soil to a flask of sea-water containing ample phosphate and nitrate increased the growth of diatoms in it.

Mention should also be made of the successive outbursts of diatom growth in the sea, where one dominant species dies out to be replaced by another, and of how diatoms cultured in flasks tend after a time to die out, particularly if bacteria become numerous.

The experimental investigation of influences affecting the growth of diatoms *in vitro* cannot by itself solve the questions which arise from observations such as these. However, the effect of some chemical factors on the rate of growth lends itself to such investigation, and was undertaken in the hope that further knowledge of the physiology of diatoms may open up new lines of enquiry.

EXPERIMENTAL METHODS.

The diatom *Nitzschia closterium* was chosen as it grows well, is persistent, and was obtainable free from flagellates. On the other hand it is a neritic species typical only of inshore waters.

I am indebted to Dr. E. J. Allen for the parent culture, which had in its turn been subcultured over a number of years. Up to the present time a persistent culture of marine diatoms has never been obtained completely free from bacteria. In interpreting these experiments, the possibility has always to be borne in mind that differences in the rate of growth of the Nitzschia may have been caused by changes in the bacterial flora or their secretion into the water. It would seem, however, that the additions of the various substances to the sea-water act directly upon the diatoms, rather than indirectly through the bacteria, but this is, of necessity, a matter of opinion.

In order to follow the rate of growth, six flasks (A, Fig. 1) of equal volume, 293 c.c., were arranged in a carrier. Each was filled with the same culture and 20 c.c. withdrawn, leaving 273 c.c. of liquid and 20 c.c. of air. To one, acting as control, a trace of mercuric chloride or potassium cyanide had been added. The carrier was placed in a water bath kept at constant temperature, usually 16° C., and the whole continuously shaken to and fro by means of a motor. The shaking was sufficient to bring the gases in solution in the liquid into equilibrium with the 20 c.c. of air within a short time. The upper ends of the gauge tubes B were connected to a manometer and the pressure adjusted so that the height of liquid in the gauge tube of the control was at a convenient mark : then the heights in the other tubes were read, the motor being stopped meanwhile. The mark on the gauge tube of the control is so chosen that the 20 c.c. of air in the series of flasks is roughly at normal atmospheric pressure.

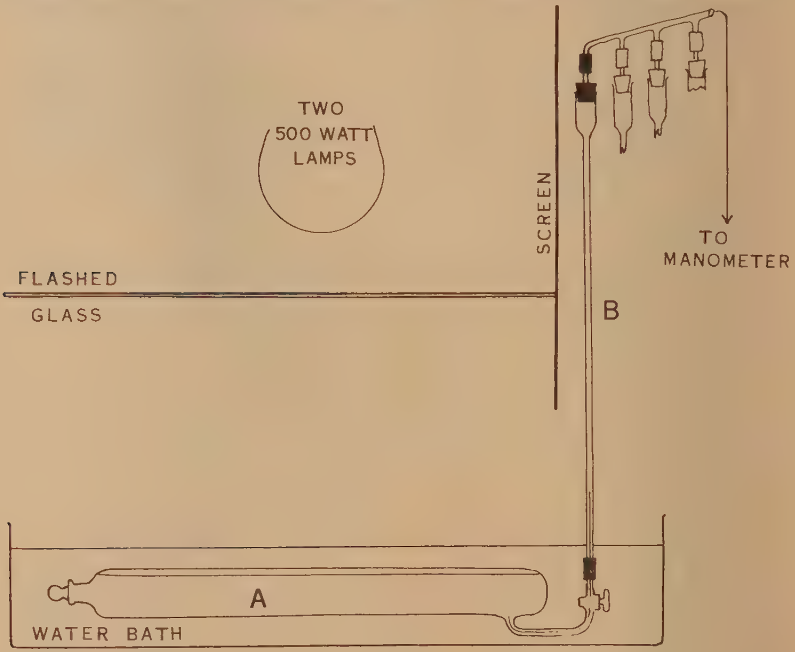

Fig. 1.

Illumination was obtained from two 500-watt gas-filled lamps with the light source 35 cm. above the tubes, and having a sheet of flashed glass immediately below the lamps. This provided more even illumination and reduced the heat radiated to the water bath. On the other hand it reduced the illumination some 50%. After a period of illumination the motor was again stopped, the manometer again adjusted so that the height of liquid in the control flask gauge was the same as before, thus obliterating the effect of any slight variation in temperature, and the heights in the other tubes read. The increases in height from the previous readings gave the increases in volume of the air above each flask, due to the oxygen given off by the diatoms. This distributes itself between the liquid and the air, increasing the volume of the latter.

The volume of oxygen produced per litre of liquid in each flask, subsequent to the first period of shaking, was calculated in the following manner.

If x c.c. of gas are evolved, mostly oxygen, it increases the volume of the 20 c.c. of air above the sea-water in the flask to $20+x$ c.c., the temperature being 16° C. and the pressure being taken as normal atmospheric pressure, the slight increase due to the rise of water in the gauge tube being neglected. Since the proportion of nitrogen in this air is slightly reduced by the oxygen given off, its partial pressure falls and a little nitrogen is given off from the sea-water. Let a c.c. be the nitrogen and $x-a$ c.c. be the oxygen evolved. The 273 c.c. of sea-water at 16° C. and normal atmospheric pressure in equilibrium with air contains 3·5 c.c. of nitrogen at 16° c. (Fox).

At the beginning the sea-water is in equilibrium with nitrogen at a partial pressure of approximately $\frac{16}{20}$ of 760 mm. Hg. After the evolution of x c.c. of gas it is in equilibrium with a mixture containing $16+a$ c.c. of nitrogen and $4+x-a$ c.c. oxygen, and the partial pressure of nitrogen becomes $\frac{16+a}{20+x}$ of 760 mm. Hg. Hence the volume of nitrogen remaining in the sea water is

$$3{\cdot}5\times\frac{(16+a)\ 20}{(20+x)\ 16}\text{ c.c.}$$

and the loss is

$$3{\cdot}5-\frac{280+17{\cdot}5a}{80+4x}=a$$

From this the gas evolved contains roughly 14% of nitrogen and 86% of oxygen.

The 273 c.c. of sea-water at 16° C. contains when in equilibrium with air at normal pressure 1·74 c.c. of oxygen measured at 16° C. (Fox). After x c.c. of gas have been evolved it is in equilibrium with the $20+x$ c.c. of gas mixture containing $4+0{\cdot}86\,x$ c.c. oxygen. The dissolved oxygen then amounts to $1{\cdot}74\times\frac{5(4+0{\cdot}86x)}{20+x}$ c.c., being an increase of $\frac{5{\cdot}75x}{20+x}$ c.c.

Hence the total oxygen production approximates to $0{\cdot}86x+\frac{5{\cdot}75x}{20+x}$ c.c. measured at 16° C. per 273 c.c. of culture, or $\frac{78x+3x^2}{20+x}$ c.c. per litre measured at N.T.P.

If oxygen is being produced rapidly by the diatoms in the flasks there will be a certain lag in time before it attains equilibrium with the air with which the liquid is being shaken. In order to assess the error likely to arise from this cause the following experiment was carried out.

Two flasks were charged with sea-water approximately saturated with air at 16° C. and two flasks with sea-water which had been partially de-aerated. They were shaken in the water bath for 3 minutes before the first readings of the heights of liquid in the gauge tubes were read. Readings were taken at intervals. In this particular experiment the manometer was disconnected. In order to eliminate a slight change in temperature in the water bath, the readings of flask IV were subtracted from those in the other three flasks, this procedure being comparable with the use of a control flask and manometer in an ordinary experiment.

TABLE I.

Change in Volume of Air in Flasks Less Change in Flask No. IV.

	I.	II.	III.
After 10 min.	—0·451	—0·483	—0·021 c.c.
20 ,,	·506	·536	·023
30 ,,	·519	·542	·020
40 ,,	·520	·545	·020
50 ,,	·522	·546	·022
80 ,,	·520	·546	·020

The result indicates that equilibrium was quickly approached, and attained within the limit of experimental error in less than 30 minutes. In the above experiment gases were entering the water, while working with diatoms oxygen passes out of the water into the air above.

In many of the experiments qualitative differences in growth rate were observed on keeping the cultures in small flasks in a north window until a thick growth had developed. Visual inspection was sufficient to show any material differences, and this was in many instances confirmed by examination in a Dubosq colorimeter. In some cases counts were made by means of a hæmocytometer having a field of $\frac{1}{10}$ cubic millimeter. In order to obtain representative values it was necessary to count several hundred cells from each culture, or even several thousand when the difference was not very great although clearly seen on visual inspection. I am indebted to Mr. G. M. Spooner for mathematical analysis of several counts.

THE EFFECT OF DISSOLVED PHOSPHATE ON THE RATE OF CARBON FIXATION BY *Nitzschia closterium*.

Nitzschia was seeded into a flask of sea-water which had been passed through a Berkfeld filter and to which an excess of potassium nitrate had been added, equivalent to over 500 mg. of nitrate nitrogen per cubic metre. This was kept in a north window until vigorous growth had used up practically all the dissolved phosphate. Analysis was made difficult by the quantity of diatoms present, but there remained certainly less than 10 mg. P_2O_5 per cubic metre. This culture was then filled into two flasks. The third, fourth, and fifth flasks were filled with the same culture to which 10, 20, and 100 mg. P_2O_5 per cubic metre had been added respectively. The sixth flask, acting as a control, was filled with the same culture to which a little cyanide had been added. Exactly 20 c.c. was withdrawn from each. After standing overnight in the dark they were illuminated and shaken at 15° C., the first reading being taken 45 minutes later.

TABLE II.

EXCESS OF PHOTOSYNTHESIS OVER RESPIRATION.
c.c. oxygen produced by 1 litre during

	1 hr. 30 min.	2 hr. 25 min.	4 hr. 20 min.	6 hr. 20 min.
Without addition of phosphate . . .	0·12	0·24	0·49	0·67
Ditto . . .	0·15	0·26	0·53	0·75
With 10 mg. per m^3 P_2O_5 added . . .	0·19	0·32	0·66	0·96
20 mg.	0·24	0·41	0·76	1·24
100 mg.	0·25	0·43	0·85	1·26

These values indicate that the addition of phosphate caused an increased rate of photosynthesis as soon as illumination was commenced, having had all night in the dark in which to be absorbed by the diatoms.

With the aim of ascertaining the final increase in fixed carbon due to the addition of phosphate, two experiments were made. Nitzschia was grown in filtered sea-water enriched with nitrate until all, or practically all, the dissolved phosphate had been used up, as shown by analysis. The flasks were filled, the control poisoned with cyanide, 20 c.c. withdrawn from each, and they were brought to constant temperature in the water bath. After a short period of illumination to ascertain that the rate of growth in all was the same within the limits of experimental error, additions of potassium hydrogen phosphate were made to three of the tubes, an equal quantity of liquid being withdrawn. They were then subjected to alternating periods of light and darkness.

Figure 2 shows the rate of growth, that is the excess of photosynthesis over respiration, during illumination. The volumes of oxygen used up in the process of respiration during the periods of darkness do not enter into the values plotted.

It is seen that growth proceeds at a steady slow rate in the tubes having no added phosphate. The increase in rate due to the addition of 20 or 86 mg. P_2O_5 per cubic metre remains about the same for 10 hours or more, after which the effect of 86 mg. becomes markedly greater than the effect of 20 mg., although even after 20 to 25 hours only a small part of the 20 mg. has presumably been used up.

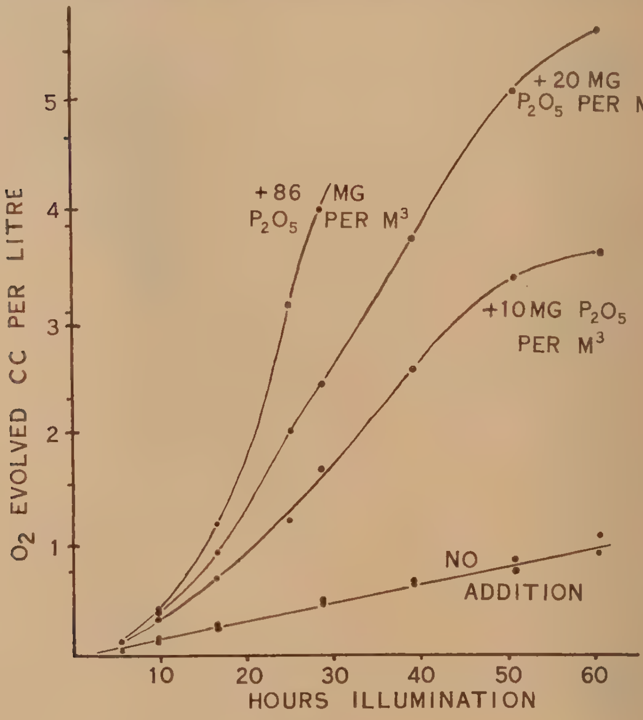

Fig. 2.

The last part of the curve, showing the growth where 10 mg. P_2O_5 per cubic metre had been added, runs parallel with the line or curve showing the growth of the diatoms without added phosphate. This indicates that the 10 mg. per cubic metre had all been utilised and that it gave rise to 2·6 c.c. per litre of oxygen more than in the tubes having no added phosphate. However, the respiration during the periods of darkness was greater in the flasks with added phosphate, the nett productions of oxygen being as follows :

TABLE III.

Nett Oxygen Production at the Expiration of 60 h. 45 m. Light and 69 h. 45 m. Darkness.

With no addition . . .	0·40 c.c. per litre.
Ditto	$0{\cdot}43_5$,, ,,
With 10 mg. P_2O_5 per m.^{3} added	2·45 ,, ,,

This shows a nett increase of 2·0 c.c. per litre due to the addition of 10 mg. P_2O_5 per m^3.

In the next experiment filtered sea-water with excess of nitrate was seeded with Nitzschia and after some days in a north window filled into five of the flasks, one of which was poisoned with mercuric chloride and used as control. In order to deduce when practically all the phosphate was used up, and to see that all the flasks behaved alike, they were illuminated daily for about 12 hours for four days. The observed increases in volume were 0·445, 0·447, 0·435, 0·440 c.c. respectively, showing remarkably close agreement. To two flasks 10 mg. P_2O_5 per cubic metre was then added, and illumination continued daily for eight days, by which time the rate of growth was the same. The oxygen production, being the nett excess of assimilation over respiration during this eight-day period of alternating light and darkness, was as follows :

Without added phosphate	1·80 1·50	mean $1{\cdot}6_5$ c.c. per litre.
With 10 mg. P_2O_5 per m.^{3}	3·9 3·9	mean 3·9 c.c. per litre.

The nett increase in oxygen, due to the addition of 10 mg. P_2O_5 per m.^{3}, is here $2{\cdot}2_5$ c.c. per litre, a value comparable with that of 2·0 c.c. found in the previous experiment.

A peculiar inference arises from these values. The addition of 10 mg. P_2O_5 per cubic metre gave rise to an observed increased growth equivalent to $2{\cdot}0\text{–}2{\cdot}2_5$ c.c. evolution of oxygen, or assimilation of the same quantity of carbon dioxide per litre, that is to say a fixation of 1·07 to 1·2 gm. of carbon per cubic metre. If the illumination had been continuous there is reason to suppose that this quantity would have been greater, the losses due to respiration during the periods of darkness being eliminated. The ratio of P_2O_5 added to carbon fixed is $\frac{1}{107}$ to $\frac{1}{120}$; even less if illumination were continuous. There are no analyses showing the ratio of P_2O_5 to carbon in the cells of *Nitzschia closterium*, but Raben's analyses of plankton consisting almost entirely of mixed diatoms gives a ratio of about $\frac{1}{15}$. The addition of phosphate brought about the fixation of seven times the amount of carbon that might have been expected.

THE EFFECT OF ADDED PHOSPHATE UPON THE RATE OF OXYGEN CONSUMPTION BY *Nitzschia closterium* IN DARKNESS.

Filtered sea-water, enriched with potassium nitrate, was seeded with *Nitzschia closterium* and kept in a north window until vigorous growth had developed. This was filled into the flasks, to three of which additions of phosphate were made. They were then covered with black cloth and shaken continuously at 16° C. in darkness. The results of this experiment are shown in Figure 3.

A second experiment was made in the same manner, but over a longer period of time. As in the previous experiment the oxygen consumption was roughly doubled where 200 mg. P_2O_5 per cubic metre had been added. The increase in rate of oxygen consumption tended to wane about 45 hours after its addition.

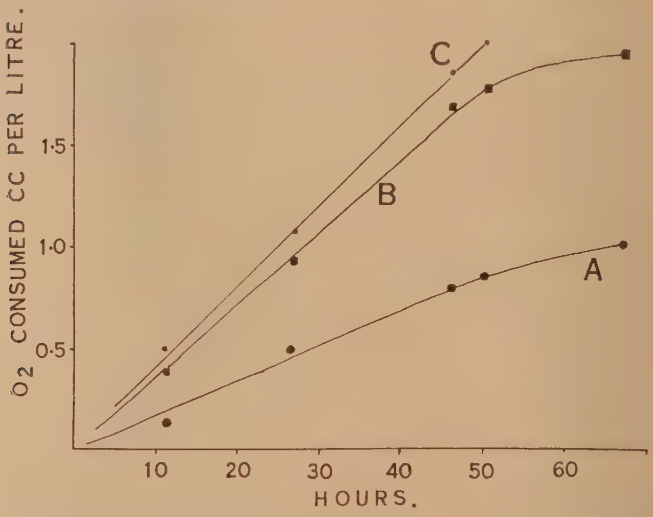

FIG. 3.—Oxygen consumption by Nitzschia in sea-water with excess nitrate in darkness. Curve A shows mean values for two flasks without addition of phosphate. Curve B shows mean values for two flasks with 200 mg. P_2O_5 per cubic metre added. Curve C shows values for flask with addition of 1000 mg. P_2O_5 per $m.^3$.

In another experiment the flasks were filled with a culture rich in nitrate which had used up practically all the available phosphate. They were exposed to alternating illumination and dim light, not complete darkness in this case. By taking the rate of photosynthesis as equal to the rate of oxygen produced under illumination plus the rate of consumption in dim light, as approximating darkness, the results may be epitomised as follows :

Rate of Photosynthesis, c.c. O_2 per litre per hour, mean of Values from two flasks in each case.

	During first day	second day	third day of experiment.
Without addition . .	0·051	0·045	0·041
With 10 mg. P_2O_5 per m.^{3} .	0·081	0·089	0·087
Mean rate of oxygen consumption in dim light :			
Without addition . .	0·008	0·011	0·013
With 10 mg. P_2O_5 per m.^{3}.	0·017	0·022	0·022

From this it appears that the rates both of photosynthesis and of oxygen consumption in darkness are about doubled by providing phosphate even in such small quantity. It is improbable that the increases are wholly due to the increase in quantity of fixed carbon brought about during the periods of illumination, particularly as the first period only gave rise to a very small carbon dioxide assimilation.

Another experiment was made in the same way. Adding 10 mg. P_2O_5 per cubic metre about doubled the rate of oxygen consumption as in the previous experiment. Treating the values in the same way, and making the same assumptions, the rate of photosynthesis increased from nearly double to over treble during the third day. In the previous experiment it remained about double. More phosphate, 86 mg. per cubic metre, rather more than doubled the rate of oxygen consumption and this rate increased as a material quantity of new growth was formed.

Rate of Photosynthesis, c.c. oxygen per litre per hour.	During first day	second day	third day of experiment.
Without addition . .	0·026	·028	·028
With 10 mg. P_2O_5 per m.^{3} .	·048	·078	·10
20 ,, ,, ,, .	·050	·10	·15
86 ,, ,, ,, .	·056	·15	·29

In these experiments the rate of oxygen consumption in darkness is due to respiration by the diatoms and to bacterial and autolytic breakdown of dissolved organic matter. However there is no reason to suppose that the addition of these minute traces of phosphate affects the bacteria and oxidation of dissolved organic matter, and it seems safe to assume that the big differences found in the rate of oxygen consumption are due to the influence of phosphate upon the respiration of the diatoms.

It is considered that they had loaded up with fixed carbon in the form of storage products, which they could not convert into new growing tissue for lack of necessary phosphorus. As soon as this is provided the conversion takes place and in consequence the rate of respiration increases. The following experiments indicate that this conversion is accompanied by division of many of the cells, and the formation of new pigment, even if the diatoms are kept in the dark.

A culture of Nitzschia in filtered sea-water, heavily enriched with nitrate, was kept for several days in a window until growth had apparently ceased owing to lack of phosphate. This was divided between two flasks, to one of which phosphate was added to the extent of 100 mg. per cubic metre. Both were then kept in darkness for 48 hours. The addition of phosphate resulted in a 29% increase in the number of diatom cells, and the culture was browner in colour than the flask to which no addition had been made.

The experiment was repeated with a fresh culture. The addition of phosphate, after 48 hours in darkness, resulted in a 28% increase in the number of diatom cells. Equal quantities were filtered and the pigment washed out from the diatoms on filter papers by repeated passage of 80% acetone. Colorimeter readings of the two pigment extracts—yellow-green in colour—showed 45% more pigment in the culture to which phosphate had been added.

A consideration of Table II, p. 259, which is typical of several experiments where the culture stood some 18 hours in the dark with added phosphate before being illuminated, is suggestive. Hand in hand with the change of stored material into actively respiring protoplasm, the photosynthetic activity of the cells was increased. During the first hour and a half's illumination the effect of adding phosphate 18 hours previously is marked.

THE EFFECT OF NITRATE AND OF AMMONIUM UPON THE GROWTH OF *Nitzschia closterium*.

The results of two experiments with cultures of Nitzschia, in sea-water enriched with phosphate, are shown in Tables IV and V. It is seen that ammonium-nitrogen replaces nitrate-nitrogen in the case of this neritic diatom, and that its addition is equally effective in promoting growth.

TABLE IV.

OXYGEN IN C.C. PER LITRE PRODUCED DURING CONTINUOUS ILLUMINATION.

	After 18½ hr.	42½ hr.	90½ hr.	138½ hr.	Increase due to addition.
No addition . . .	0·37	0·85	1·06	1·2	
With addition of 60 mg. per m.^{3} of nitrate/N_2 .	0·52	1·7	2·4	2·5	1·3
60 mg. per m.^{3} of ammonium N_2 ammonium .	0·51	1·8	2·7	3·1	1·9

TABLE V.

Oxygen, c.c. per Litre, Produced After

	7 hr. illumination 24½ hr. darkness 21 hr. illumination	54 hr. illumination 24½ hr. darkness	93 hr. illumination 24½ hr. darkness	Increase due to addition.
No addition	0·7	2·8	4·0	
60 mg. per cubic metre nitrate–N_2 added .	1·08	4·0	5·15	1·15
Ditto	1·16	4·2	5·45	1·45
60 mg. per cubic metre of ammonium N_2 added	1·08	4·0	5·23	1·23

The increase in oxygen production brought about by this addition of 60 mg. per cubic metre of nitrate-nitrogen in these two experiments was 1·3, 1·15, 1·45 c.c. per litre, the mean being equivalent to the fixation of 0·7 gm. carbon per cubic metre. The ratio of nitrogen added to carbon fixed is therefore $\frac{1}{12}$.

Analyses by Raben of plankton consisting mainly of mixed diatoms gave a ratio of nitrogen to carbon amounting to roughly $\frac{1}{5}$. As with phosphate, the addition of a small quantity of available nitrate gives rise to an unexpectedly large increase in the amount of carbon fixed.

During the vernal outburst of diatoms in the sea about two and a half times more nitrate-nitrogen than phosphate (as P_2O_5) is used up. Yet in these experiments the addition of roughly ten times more nitrate-nitrogen than phosphate is required to bring about the same increase in fixed carbon.

Under the conditions of these two experiments the addition of ammonium brought about a similar increase in growth to that brought about by the addition of nitrate.

The Effect of Arsenate upon the Growth of *Nitzschia closterium.*

The quantity of phosphate in sea-water as estimated by the Atkins-Denigès method includes any arsenate which may be present. After vigorous growth of phytoplankton in the summer, the phosphate content of the water, estimated by this method, may fall to less than 1 or 2 mg. P_2O_5 per cubic metre. Hence there is either practically no arsenic present as arsenate or the phytoplankton utilises it. With regard to the latter possibility, it is known that some plants can utilise arsenate partially in lieu of phosphate. In a single preliminary experiment, made in 1930 in daylight with rather crude apparatus, increased growth was observed due to the addition of sodium arsenate amounting to 20 mg. As_2O_5 per cubic metre. However, in six instances, when between 20 and 40 mg. As_2O_5 per cubic metre were added and the experiments carried out in the apparatus here described, the rate of photosynthesis was reduced.

EFFECT OF HYDROGEN ION CONCENTRATION.

An experiment was made with a vigorous dense growth of Nitzschia in filtered sea-water which had been enriched with phosphate and nitrate. The pH was reduced to varying degrees by blowing alveolar air through the culture. The oxygen production during illumination is shown in the following table.

TABLE VI.

Approximate pH measured colorimetrically. Initial.	Final.	c.c. oxygen produced per litre during 3 hr. 45 min. illumination.
8·4	8·45	0·48
8·1	8·1	0·50
7·9	7·9	0·57
7·45	7·4	0·55
less than 7·0		0·55

This experiment indicates that slight variations in pH in the tubes of culture are not likely to have invalidated any of the foregoing experiments.

THE EFFECT OF EXCESS BASE.

In many of the following experiments rich cultures were produced in small flasks where, from the nature of the experiment, the rate of growth may have been gradually slowed owing to excessive rise in pH. Since the addition of any base would hinder the rise in pH by increasing the buffering, it was desirable to find out if the addition of any substances used in the experiment had acted by altering the " excess base " in the sea-water and so affecting its buffering capacity. With this end in view an experiment was made in which a solution of sodium bicarbonate saturated with carbon dioxide was added to flasks of enriched sea-water inseminated with Nitzschia. This increased the excess base to ·0036, ·0046, and ·0086 Normal. No significant effect was noticeable upon the growth of Nitzschia.

THE EFFECT OF IRON.

Filtered open sea-water was enriched with phosphate and nitrate and inseminated with Nitzschia. Varying quantities of ferric ammonium citrate were added to flasks of this. After two days in a north window the effect of added iron was noticeable. On the ninth day the cells were counted by means of a Hæmocytometer with the following result :

Iron added. Mg Fe per c.m.	Number of cells per cubic mm.
none	5,340
8	7,070
80	9,540
1,600	13,870

It was realised from other experiments proceeding simultaneously with this one that the full effect of added iron was probably suppressed owing to lack of silicate. The cultures are thick and the diatoms require more than is initially present in the water (200-400 mg. SiO_2 per $m.^3$) and is being continually dissolved from the glass of the flasks.

A similar experiment was made in which the water was enriched with silicate as well as with phosphate and nitrate, and three series of flasks set up with additions of ferric ammonium citrate. After fifteen days in a window counts were made in one series with the following result :

Iron added. MgFe per c.m.	Number of cells per cubic mm.
none	7,370
1 mg.	16,360
3 mg.	16,540
5 mg.	28,000

From inspection as growth was proceeding in the three series of flasks it was clear that the rate of growth was about doubled in each case by the addition of 1 mg. Fe per cubic metre.

An experiment was made with a vigorous thick culture, in water enriched with phosphate nitrate and silicate, to see if the addition of iron caused division of the cells or formation of colouring matter when kept in the dark, but no evidence of this was found.

A number of experiments were made with the object of indicating in what form iron is available and effective. Iron ammonium citrate is slowly hydrolysed in sea-water, less rapidly if sodium citrate is also added, when it remains longer in solution as an " iron-citrate " complex. The addition of sodium citrate did not make a culture with iron ammonium citrate grow any faster, which indicates that the " iron citrate " complex itself is not available to the plants—a conclusion also arrived at by Hopkins (**13**). With regard to other iron compounds an experiment was made in which 800 mg. Fe per cubic metre was added in the form of ferric ammonium citrate (slowly hydrolysed), ferric alum, ferrous sulphate (both rapidly hydrolysed in sea-water) and dialysed iron, the colloidal hydroxide formed by hydrolysis. The citrate was most immediate in its action, but after twelve days in a window the iron alum and ferrous sulphate had brought about an increased growth similar to that due to the addition of citrate. Dialysed iron in this and other experiments was found to have no effect or only very little. Gran had found that hæmoglobin was without effect and the writer that hæmatin likewise did not promote growth. A small piece of steel was found to improve the growth in a culture, as it rusted. It would seem that these additions act through the iron-ions which they give off and which escape hydrolysis to the unavailable hydroxide.

The writer was unable to detect any ferric or ferrous ions in sea-water until it had been both made acid and subjected to vigorous oxidation, as by boiling with bromine water. It would seem that it mostly occurs as organic compounds (**14**) in solution and ferric hydroxide in suspension or colloidal solution (**4**), with only a small moiety in a form available to plants.

These experiments as a whole indicate that iron in an available form does not exist in sea-water in sufficient quantity for the most rapid growth of Nitzschia. There is sufficient, however, for a heavy final production. There is no evidence whether this is present *ab initio* or is formed from " unavailable iron " as the " available " is used up.

We have found that the addition of 1 mg. Fe per cubic metre in the form of citrate doubles the rate of growth of Nitzschia. Probably much of this addition exists in the form of iron-citrate complex and the hydroxide formed from it by hydrolysis, neither of which appear to be "available." It does not seem unreasonable to conclude from this that sea-water contains less than 1 mg. per cubic metre of iron in an available form. Analysis shows that the concentration of iron-ions is less than this amount. Hopkins considers that iron-ions are the only form in which iron is available, basing his conclusion on experiments with the freshwater alga Chlorella, which however requires much more iron for growth than do marine diatoms. He estimates that Chlorella requires some 82 mg. iron-ions per cubic metre in the culture solution to give satisfactory growth.

The Effect of Added Silicate.

The filtered sea-water used in these experiments contained silicate in solution to the extent of 200–400 mg. SiO_2 per m.^{3}. A further supply of silicate arose from the glass vessels. Sea-water is known to dissolve silicate from glass, and after long use the flasks are seen to be corroded.

In a number of cases it was noticed that with a thick culture in glass flasks—2,000 to 5,000 cells per cubic mm.—increased growth was obtained if the water had been enriched with sodium silicate (2,000 mg. SiO_2 per cubic metre) in addition to phosphate and nitrate. The cells were rather larger and more regular in shape.

The solution of silicate from the glass was demonstrated in an experiment where sea-water inseminated with Nitzschia and enriched with phosphate and nitrate was kept in a north window in glass bowls. Two of the bowls were coated with paraffin wax inside while two were coated outside in order that the illumination in all four should be similar. During the first days there was no noticeable difference, but in seven days the growth had become significantly greater in the bowls which were waxed outside and where the water was free to dissolve silicate from the glass.

The Effect of a Previous Growth of Nitzschia in the Culture Medium.

A rich culture of Nitzschia was prepared in filtered sea-water enriched with phosphate and nitrate. This culture, several weeks old, was filtered through a membrane filter and the filtrate saturated with air. As control a sample of sea-water was filtered in the same way. Both were enriched with excess of phosphate and nitrate, then seeded with the same quantity of Nitzschia, and kept in a window. Growth was significantly greater in the water filtered from the previous growth of Nitzschia.

The experiment was repeated except that a Nitzschia culture was filtered as soon as a thick vigorous growth had taken place. The filtrate was low in dissolved silica, containing 210 mg. SiO_2 per cubic metre, while the control contained twice this amount. In this case rather more growth was obtained in the control than in the filtrate from the vigorous culture. However, when a trace of sodium silicate was added to both, bringing the SiO_2 content up to about 2,000 mg. per cubic metre in each case, significantly greater growth was obtained in the filtrate from the culture.

These experiments indicate that Nitzschia does not secrete substances into the surrounding water which are inimicable to the further growth of the same species, but rather that the cells secrete substances which accelerate growth.

The Effect of Soil Extract upon Growth.

The influence of land drainage running into the sea upon the growth of diatoms has been noticed since many years. It used to be attributed to the supply of phosphates and nitrogen salts carried down from the soil, but the more recent analyses show that these often amount to little and that their effect would not extend far seaward. Gran suggests that land drainage acts largely by reason of the iron salts and colloidal iron which it brings into the sea, possibly also manganese. Atkins showed that it provides silicate, lack of which may hinder diatom growth, perhaps even preventing it in the open oceans of low latitude far from land, where diatoms give way to coccolithophores.

It has long been known that the growth of diatoms and other plants, moulds and other organisms in culture solution is accelerated by the addition of a little vegetable or soil extract (Miquel, Allen, Pasteur, Wildiers, Schreiber, Nielsen and Hartelius and others). It appears that some organic substance or group of substances, occurring rather widely in the breakdown products of living organisms, acts as a growth-promoting factor.

The foregoing experiments show that the silicate in solution in a soil extract may often increase growth, even in cultures in glass vessels from which silicate is continuously though slowly given off. They show that diatom growth will be accelerated if the addition of soil extract to sea-water increases the available iron. No experimental evidence has actually shown that it adds to the available iron, although this seems probable.

It is yet an open question what constituents of land drainage other than silicates, phosphates, nitrogen salts and perhaps iron influence diatom growth in the sea. The following experiments were made with the aim of throwing more light upon this.

Soil extract was prepared by boiling garden soil with water, filtering and bringing this filtrate to boiling point at intervals of two days or more to destroy bacteria.

Filtered sea-water, heavily enriched with phosphate and nitrate, about 1,000 mg. P_2O_5 and 3,000 mg. nitrate-nitrogen per cubic metre, was seeded with Nitzschia and 60 c.c. portions poured into five small flasks. Addition of soil extract was made to four of these. They were kept in a north window at room temperature for nine days, when the number of cells was great enough to make fairly accurate counting possible.

TABLE VII.

NUMBER OF CELLS PER CUBIC MILLIMETRE.

	After 9 days.	Increase due to addition
No. addition . . .	860	
0·05 c.c. soil extract . .	1,030	170
0·10 c.c. ,, ,, . .	1,230	370
0·5 c.c. ,, ,, . .	1,380	520
2·0 c.c. ,, ,, . .	1,770	910

The increased growth was very apparent on inspection only, the colour of the culture being browner and the turbidity due to the tiny cells more marked. Later, as growth proceeds, the differences between the flasks became less noticeable—the cells tend to clump together and to adhere to the bottom and sides of the flasks, making accurate counting impossible.

Experiments were then made to investigate the effect of soil extract on the rate of growth and of respiration of an actively growing culture of Nitzschia in enriched sea-water. Table VIII shows the effect of 3 hours illumination, followed by 18 hours darkness, followed by 4 hours illumination and then 18½ hours darkness.

TABLE VIII.

OXYGEN PRODUCTION + OR UTILISATION — IN C.C. PER LITRE DURING PERIODS OF

	3 hr. illumination.	18 hr. darkness.	4 hr. illumination.	18½ hr. darkness.
No addition . . .	+1·14	—0·48	+2·4	—0·68
No addition . . .	+1·14	—0·48	+2·4	0·60
With 0·5 c.c. soil extract .	+1·14	—0·53	+2·9	0·60
2·0 c.c. ,, ,, .	+1·16	—0·65	+3·3	0·68
5·0 c.c. ,, ,, .	+1·14	—0·75	+3·3	0·78

It is seen that soil extract did not affect the rate of photosynthesis during the first 3 hours illumination—it is not immediate in its effect. The respiration rate after this short period of illumination was however increased. The rate of photosynthesis was increased during the ensuing period of 4 hours illumination but the rate of respiration during the ensuing period of darkness was not materially affected.

The increase in respiration after the first short period of illumination is peculiar. The values are significant and regular. In order to see if it was due to the oxidation of the soil extract, the experiment shown in Table IX was made. Two flasks were charged with a rich growth of Nitzschia in enriched sea-water and two with filtered sea-water without diatoms. To one of each soil extract was added. After 48 hours shaking in darkness at 16° C. the lights were turned on to make sure that the soil extract was effective in promoting photosynthesis.

TABLE IX.

OXYGEN UTILISED —, IN C.C. PER LITRE

	After 24 hr. darkness.	After 48 hr. darkness.	Oxygen produced during subsequent period of 6 hr. illumination.
No addition	—1·25	—2·68	+2·2
With 5 c.c. soil extract . .	—1·31	—2·76	+3·3
Filtered sea-water only . .	—0·10	— ·17	
Ditto, with 5 c.c. soil extract .	—0·15	— ·32	

Slow oxidation of dissolved organic matter in the filtered sea-water is demonstrated, greater where soil extract had been added. Taking this into account the values show that the addition of soil extract had no appreciable effect upon the rate of respiration, although the added soil extract was very effective in promoting photosynthesis during subsequent illumination.

The next step was to find whether addition of soil extract caused division of the cells or formation of colouring matter in darkness. Filtered sea-water was enriched with phosphate and nitrate, inseminated, and after a vigorous growth of Nitzschia had developed divided into two portions. To one 10% of filtered sea-water was added, to the other 10% of an extract of soil made with sea-water. They were then kept in the dark for 48 hours and the cells counted by means of a hæmocytometer. This experiment was repeated three times with the following results :

NUMBER OF CELLS PER CUBIC MM.

	With soil extract.	Without.	Increase.
Experiment I . .	1,540	1,320	16%
,, II . .	5,630	4,840	16
,, III . .	1,630	1,490	9

There was no noticeable increase in colouring matter due to the addition of soil extract.

A series of experiments indicated that soil extract did not act only through the silicate and iron which it contains. Filtered sea-water was enriched with phosphate, nitrate, silicate and iron (80 mg. Fe per cubic metre in the form of ferric ammonium citrate), and inseminated with Nitzschia. Growth was rapid and the final production great, yet the addition of soil extract caused a material increase in the rate of growth. There is reason to suppose that this increase was not due to the extra silicate and iron added in the soil extract, since there was already a large excess of silicate and a heavy enrichment with iron in the control.

That iron does not play the leading rôle is further suggested by the observation that an alkaline extract of soil is more effective than an acid one, both being neutralised previous to use.

There is indication that the growth-promoting factor is of organic nature, possibly a group of organic substances, often present in the break-down products of animal or vegetable matter. Thus evaporation and ashing of soil extract destroys its growth-promoting properties. The addition of a very small quantity of yeast or Fucus or Nitzschia extract or of a very dilute solution of ovolecithin promoted growth in a culture rich in phosphate, nitrate, silicate and iron.

THE EFFECT OF ICE WATER.

A suggestion has been made by Barnes (**15**) that the production of diatoms may be influenced by trihydrone molecules in the water from recently melted ice or snow. He found that Spirogyra grew more rapidly in water which had been previously frozen than in water which had recently condensed from the gaseous state, and even than in water which had long been in the liquid state. In this preliminary communication details of the control of other factors, such as the supply of nutrient salts, are not given.

It is easy to experiment with Nitzschia in such a way that the only variables are the possibly different nature of the water molecules. Filtered sea-water was enriched with phosphate, nitrate, iron citrate, and sodium silicate and inseminated with the diatom. Fifty c.c. portions of this were filled into small flasks, to half of which were added 10 c.c. of recently distilled water and to the other half 10 c.c. of the same water which had been frozen and allowed to melt. The flasks were then kept in a north window at room temperature, which varied around 20° C. Between each pair of flasks the only difference was that recently distilled water had been added in the one case, and water from melted ice in the other.

The experiment was repeated several times and, except in the case of one pair of flasks, a greater growth could be distinguished after several days where ice water had been added. Counts were made of the number of diatoms in one pair of flasks after five days' growth with the following result :

With recently distilled water, 4,310 cells per cubic mm.
With recently distilled water previously frozen and melted, 5,430 cells per cubic mm.

In this experiment, with two pairs of flasks, the difference was very clearly distinguishable, equally so in each pair. In other experiments the difference was not always so marked although distinguishable.

The question was attacked in another manner. Filtered sea-water similarly enriched was filled into two flasks. One was partially frozen and allowed to attain room temperature. Then both flasks were inseminated with the same quantity of a thin Nitzschia culture and kept in a north window. In each of the experiments the growth was perceptibly greater in the water which had been partially frozen. It is possible that a minute trace of some constituent separated out from solution when the latter concentrated during the partial freezing, so these experiments do not form such good indication of the possible physiological action of trihydrone as the former series appear to do.

These experiments were all made at room temperature during the summer months under conditions of good illumination, the daylight lasting some 15 hours out of the 24.

A similar series of experiments was made in November, also at room temperature, the illumination being weaker and lasting only some 9 hours out of the 24. No difference was detected between the flasks with added ice water and the controls although good growth had taken place in a week.

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SUMMARY.

The neritic diatom *Nitzschia closterium* was grown at constant temperature under artificial illumination in filtered sea-water to which various additions had been made. The oxygen production or utilisation was measured by observing the change in volume of air with which the cultures were continuously shaken.

The addition of phosphate to a culture poor in this nutrient salt increased the rate of both photosynthesis and respiration.

If kept in darkness after the addition of phosphate, an increase in number of cells and of yellow-green pigments resulted.

The addition of 1 part P_2O_5 gave rise to an increased carbon fixation of 107 to 120 parts of carbon.

The addition of nitrate and ammonium increased the rate of photosynthesis.

The addition of 1 part nitrate-nitrogen gave rise to an increased carbon fixation of 12 parts of carbon.

The addition to sea-water, enriched with phosphate, nitrate, and silicate, of 1 mg. Fe per cubic metre in the form of citrate doubled the rate of growth.

The addition of silicate increased the production of Nitzschia in glass vessels from which the culture solution only slowly dissolves silica.

Experiments bearing on the effect of a previous growth of Nitzschia in the culture solution are described.

The addition of a sterilised extract of garden soil increased the rate of photosynthesis. It also caused multiplication of cells in the dark. Evidence is given suggesting that this may be due to the provision of silica and possibly iron in a form readily assimilated by diatoms, and also to a "growth-promoting factor."

Some evidence is given that the growth of Nitzschia proceeds faster,

under certain conditions, in water part of which had recently been in the form of ice.

The conclusions are tentative in that they are based on a limited number of observations of one species of diatom under a narrow range of experimental conditions; moreover, it is not improbable that this species may behave differently under different conditions, as of light, temperature, age and volume of culture. The aim of this preliminary investigation was to suggest new lines of enquiry and supplement current research concerning the productivity of the sea, rather than to study the effect under a wide range of conditions of any one factor upon this diatom.

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The Food Consumed by Shags and Cormorants around the Shores of Cornwall (England).

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With 2 Figures in the Text.

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I. INTRODUCTION.

AT a meeting held in the County Hall at Truro, Cornwall, on 30th August, 1911 (2, *a*), the Cornwall Sea Fisheries Committee decided to offer a reward of one shilling for the head of every Shag and Cormorant killed within the limits of the sea fisheries district under the jurisdiction of the Committee, the reward to become payable on and after the first day of September—just two days later.

This action was taken as the result of many and bitter complaints having reached the Committee concerning the destruction of marketable fishes—especially young flatfishes—by these birds in Cornish waters. Within one month after the initiation of this scheme for reducing what was then believed to be a serious menace to Cornish inshore fisheries, 751 birds' heads were received. Although this heavy initial slaughter did not for long continue unabated, the Fishery Officer for the County, in his quarterly report submitted to the Committee at their meeting on 26th May, 1915 (2, *e*), stated that he had then paid for a total of 4,220 birds since the order was first issued in September, 1911. He also further stated in that report that "from information gathered along the coast it is the general opinion of the longshore fishermen that since the destruction of so many of these birds there is a marked improvement in the quantity of fish in our coves and estuaries."

In July, 1915 (**2**, *f*), owing to certain difficulties which had arisen in connection with the continuation of the scheme, the offer of rewards for the destruction of Shags and Cormorants was withdrawn.

The scheme was again brought into being in September, 1925 (**2**, *h*), and remained in operation until the end of 1929, when the payment of rewards was again discontinued (**2**, *j*). During this second period in which the reward was offered, 6,739 heads were received and paid for, making a total of 10,959 birds killed, payment for which had involved an outlay of approximately £550.

From time to time, while the scheme for the destruction of Shags and Cormorants was in operation, doubts were expressed in various quarters as to its efficacy, no appreciable beneficial effect having become evident in the fisheries. Apparently even the fishermen's previously avowed belief in its usefulness had also faded, for the Fishery Officer's report to the Committee, dated 12th December, 1929 (**2**, *j*), contains the following statement. "During my periodical visits throughout the County I have interviewed several fishermen as to the effect of the operation of the scheme on the fisheries. The consensus of opinion is that there is no positive evidence that the destruction of these birds has been sufficient to influence the fisheries to any appreciable extent."

This purely negative result of the Committee's action could be explained by the operation of either of two entirely different factors—(1) that although the birds are definitely harmful, their numbers had not been reduced sufficiently to have any appreciable effect upon the fish stocks; or (2) that the birds are not so harmful as the fishermen had stated and as the Committee had been led to believe. If the former explanation were the true one, the launching of a more intensive campaign against the offenders would probably have been the proper course to pursue; whereas if the latter hypothesis should be correct the destruction of the birds in the past had been entirely unnecessary and unjustifiable and ought in no circumstances to be continued.

In order to dissipate the fog of uncertainty in which the Committee had gradually become enveloped, Dr. E. J. Allen, Director of the Plymouth Laboratory, undertook to have the stomach contents of any birds sent to him examined and their food reported upon by members of his staff. Following upon this offer by Dr. Allen, 39 birds were received at the Laboratory during the autumn of 1929. They were examined by Mr. V. C. Wynne-Edwards, who submitted a report of his findings to the Committee at their meeting of 18th December, 1929. In this report Wynne-Edwards stated that "the Shags seem to be feeding almost entirely on inshore fishes and very seldom take any marketable species. Out of a total of 84 fishes which I have been able to name only 3 have been marketable and of these the one I have entered as 'Gadus sp.' was almost certainly a Poor-cod, and the 'Clupea sp.' was probably a Sprat. This leaves one small Dab on the black list."

Four of the Cormorants examined by Wynne-Edwards contained identifiable food in their stomachs but no food fishes were included. Too few birds had been examined, however, to justify his making any definite statement concerning them.

It was after consideration of this report that the Committee hurriedly issued a notice withdrawing their offer of rewards for the heads of Shags and Cormorants. At the same time, they agreed to contribute towards the cost of further investigations by the Marine Biological Association.

Shortly afterwards Mr. Wynne-Edwards left the country and the subsequent investigations have been carried out by the present writer.

The researches were continued until early in 1933, when it was considered that a sufficient number of both species had been obtained to justify definite conclusions being drawn from them concerning the normal food of these birds in this area. The total numbers of Shags and Cormorants examined in the years 1929–1933 inclusive are shown in Table I.

TABLE I.

NUMBERS OF SHAGS AND CORMORANTS EXAMINED IN EACH OF THE YEARS 1929–1933 INCLUSIVE.

	SHAGS.			CORMORANTS.		
	Stomach containing recognisable food.	Stomach empty.	Total number of birds examined.	Stomach containing recognisable food.	Stomach empty.	Total number of birds examined.
1929	23	11	34	4	1	5
1930	12	14	26	0	1	1
1931	35	8	43	1	0	1
1932	115	1	116	19	0	19
1933	3	0	3	3	0	3
Totals	188	34	222	27	2	29

II. METHODS EMPLOYED.

In 1929 birds shot from time to time in the neighbourhood of St. Austell and Mevagissey were sent to the Plymouth Laboratory for examination of their stomach contents. All the birds had been dead for some time, therefore, before their stomachs could be opened and their food recorded. Thirty-nine birds (34 Shags and 5 Cormorants) were dealt with in this way and one small Dab was the only food-fish found in them.

It was considered not unlikely that these results had been vitiated by the digestion which continues in the birds' stomachs for a considerable time after life is extinct. In order to eliminate this possible source of error arrangements were made in the summers of both 1930 and 1931 by which all birds were examined almost immediately after death. The results obtained after adopting this precaution were similar to those previously recorded. It can safely be concluded, therefore, that the 1929 results are perfectly reliable.

As most of the birds dealt with in the years 1929–31 had been shot during the summer months around rocky and exposed shores it was decided that, in order to make the investigation complete, birds shot during the winter months and in other localities ought also to be secured for examination. In the winter of 1931–32, therefore, an effort was made to obtain birds from sandy bays, harbours, and river estuaries, where flatfish are known to be numerous and where fishermen state that they frequently see Shags and Cormorants devouring large numbers of them.

By this means also it was hoped to receive a larger proportion of Cormorants than formerly when most of the birds shot were Shags. This was due to the fact that where shooting had been carried on Shags are plentiful and Cormorants relatively very scarce. The Shag is essentially marine, seldom venturing inland or even into the more or less enclosed waters of harbours and estuaries unless compelled to forsake its usual haunts by stormy weather. The Cormorant, on the other hand, normally frequents harbours, estuaries, and tidal rivers, and may even visit lakes and reservoirs far inland. Very occasionally it will venture out along the open coast but never goes far to sea.

In spite of these efforts, however, only four birds (two Shags and two Cormorants) were obtained from such localities during the winter of 1931–32, none of which contained any food-fishes.

As the following winter (1932–33) approached, a still more determined effort was made. In November, 1932, the reward offered for each bird shot in or near any harbour, sandy bay, or river estuary was increased from one shilling to two shillings and sixpence. The assistance of the Fishery Officer for Cornwall (Mr. W. H. Barron) was also enlisted. Mr. Barron was asked to select suitable men to shoot birds in specified localities around the coast and forward them to the Plymouth Laboratory. These measures were unexpectedly successful. Birds soon began to arrive in large numbers and in a very short time sufficient data had been collected to complete the investigation.

Throughout this work the numerical method of recording the stomach contents has been adopted, the number of recognisable organisms of a species or group being noted.* Many stomachs contained also a mass of highly comminuted and unrecognisable food fragments. No attempt was made to deal with this in any way. Identification of fishes from the otoliths† accumulated in the bottoms of the birds' stomachs were likewise not attempted as this was considered unnecessary in view of the numbers of food organisms directly and more accurately identifiable.

One point of considerable interest and of no little importance in the future conduct of the investigation came out clearly from the work done in the summer of 1930. Twenty-two Shags (12 adults and 10 young) were shot near Port Isaac on July 7th, all before 7 o'clock in the morning. Not one of these birds had a particle of food in its stomach; without doubt the birds had all been shot before feeding had begun. It was therefore decided that in future no shooting should take place very early in the morning. This precaution had the desired result, and very seldom afterwards were birds received whose stomachs did not contain recognisable food material.

III. Food of Shags (*Phalacrocorax graculus graculus* (L.)).

In Table II are summarised the results of the examination of the 188 Shag stomachs which contained recognisable food. It will be seen that the food consisted almost entirely of fishes, with, in addition, a very small proportion of various crustaceans. Twenty-four kinds of fish have been recognised with sufficient accuracy to place them in their Genera, and in twenty cases the species also has been determinable. Ninety-six birds—or 51 per cent of those containing recognisable food—were found to have been feeding on Sand Eels (Ammodytes spp.), and 69 of them had *nothing but Sand Eels in their stomachs.* There can be no doubt that Sand Eels constitute the staple food of Shags in this area throughout the whole year. Wrasses, Gobies, Rocklings, Blennies, Dragonets, and other non-marketable species are also regularly eaten in smaller numbers.

In the winter months, however, Sprats and other Clupeoids also enter to some extent into the diet of Shags. In one stomach approximately 200 small Clupeoids up to about 2 inches in length (recorded as Clupeoid Britt) were found. Seven birds had devoured one or more Anchovies.

The Clupeoids are marketable species but, with the exception of the Anchovy which is not fished here, they are present in such large numbers that any depletion which Shags may be able to effect cannot possibly be

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* See also Appendix II, p. 291.

† Remarkably large numbers of otoliths (up to 73) frequently were found in the stomachs. Possibly they accumulate and are used for breaking up the food in somewhat the same way as fowls and pigeons use small pebbles.

TABLE II.

Food of Shags (Summary).

Total number of birds examined 222—of which 188 contained identifiable food organisms in their stomachs.

Name of food animal.*	Number of birds in which found.	Highest number found in one stomach.	Total number recognised in all the stomachs examined.
Sprat (*Clupea sprattus*)	**20**	**50**	**278**
Anchovy (*Engraulis encrasicholus*)	**7**	**15**	**24**
Britt (Small Clupea spp.)	**2**	**200** (estimated)	**350** (estimated)
Clupeoid (Herring, Sprat, etc.) Remains	**21**	—	—
Conger Eel (*Conger vulgaris*)	**2**	**1**	**2**
Bib (*Gadus minutus*)	**2**	**1**	**2**
Pollack (*Gadus pollachius*)	**2**	**2**	**3**
Ling (*Molva molva*)	**1**	**1**	**1**
Gadoid (Gadus spp.) Remains	**3**	—	—
Dab (*Pleuronectes limanda*)	**2**	**7**	**8**
Flatfish (Pleuronectid) Remains	**3**	—	—
Sea Stickle (*Spinachia vulgaris*)	2	1	2
Pipe Fish (*Syngnathus acus*)	1	1	1
Sand Eel (Ammodytes spp.)	96	30	440
Five-bearded Rockling (*Onos mustelus*)	1	1	1
Three-bearded Rockling (*Onos tricirratus*)	8	1	8
Blenny (Blennius spp.)	1	1	1
Blenny (*Chirolophis ascanii*)	3	1	3
Weever (*Trachinus vipera*)	1	1	1
Dragonet (Callionymus spp.)	19	5	36
Goby (*Gobius flavescens*)	1	1	1
(*Gobius minutus*)	2	35	45
(Gobius spp.)	3	1	3
Sea Scorpion (Cottus spp.)	2	2	3
Ballan Wrasse (*Labrus bergylta*)	12	5	17
Cuckoo Wrasse (*Labrus mixtus*)	3	4	7
Corkwing Wrasse (*Crenilabrus melops*)	3	5	11
Gold-sinny Wrasse (*Ctenolabrus rupestris*)	24	10	63
Wrasse (Labrid) Remains	5	—	—
Comber (*Serranus cabrilla*)	1	1	1
Unidentifiable Fish Remains	28	—	—
Prawns (Palæmonidæ)	9	5	16
Shrimps (Crangonidæ)	5	2	7
Miscellaneous Crustacea	3	—	—

* Marketable fishes in heavy type.

considered to constitute a menace to any commercial fishery for them which exists in this area.

Bib, Pollack, and Ling are other species, of more or less value commercially, which are occasionally eaten by Shags, but the numbers killed in this way are so small as to be quite negligible—more especially since these fishes, though marketable, are not very valuable.

Only 5 out of the 188 birds were found to have eaten flatfish. Two of those were shot in Mevagissey Bay, one on November 2nd, 1929, and the other on November 23rd, 1932. The former had eaten one small Dab and the latter had unidentifiable flatfish remains in its stomach. The three others, it is important to note, were all shot in river estuaries. Two of them were obtained from the Camel River in November, 1932, one of which contained the remains of a single flatfish (Flounder ?) and the other had in its stomach seven small flats—five of them obviously Dabs and the two others either Dabs or Plaice. The fifth bird, shot in the

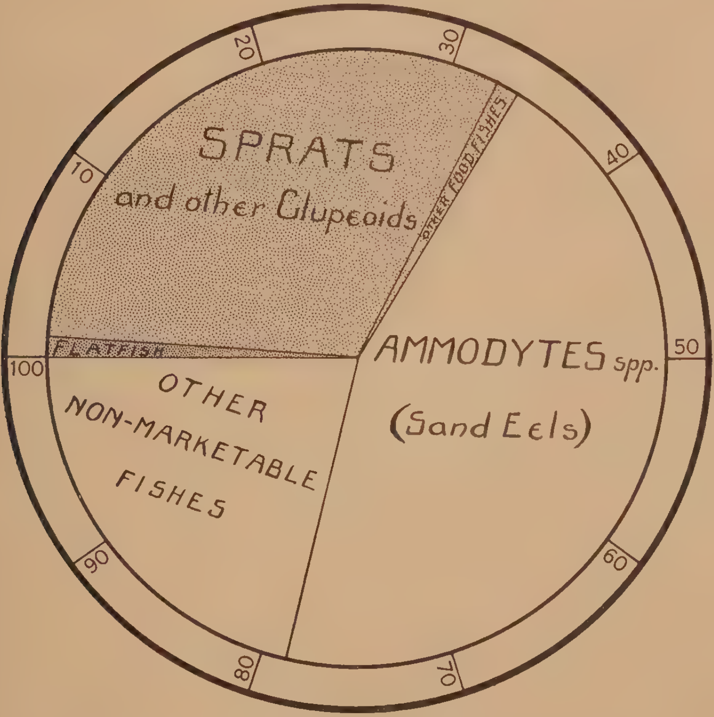

Fig. 1.—Diagrammatic representation of the percentage numerical composition of the food of Shags (Clupeoid Britt and Crustaceans omitted).

TABLE III.

Food of Cormorants.

Total number of birds examined 29—of which 27 contained recognisable food organisms in their stomachs.

Serial number of bird.	Date examined.	Locality where shot.	Herring (*Clupea harengus*).	Sprat (*Clupea sprattus*).	Freshwater Eel (*Anguilla vulgaris*).	Conger Eel (*Conger vulgaris*).	Grey Mullet (*Mugil chelo*).	Father Lasher (Cottus sp.).	Dragonet (Callionymus sp.).	Goby (Gobius spp.).	Flounder (*Pleuronectes flesus*).	Plaice (*Pleuronectes platessa*).	Dab (*Pleuronectes limanda*).	Flatfish remains.	Gurnard (Trigla sp.).	Pogge (*Agonus cataphractus*).	Ballan Wrasse (*Labrus bergylta*).	Corkwing Wrasse (*Crenilabrus melops*).	Gold-sinny Wrasse (*Ctenolabrus rupestris*).	Prawns (Palæmonidæ).	Shrimps (Crangonidæ).
	1929																				
1	July 15	Mevagissey			1				2												
6	,, 15	,, ...															1				
12	,, 26	,, ...															1				
19	September 20								1										1		
	1931																				
93	July 29	Newlyn															1				
	1932																				
113	February 4	River Erme (Estuary) . .																1	1		
114	,, 4	,, ,, ,, . .																		2	

115	October	18	Mouth of Yealm River	1																		
168	November	23	River Camel (Estuary)									8										1
172	,,	23	St. Austell Bay									1	1									
174	,,	23	,, ,,															3				
175	,,	23	,, ,,						5													+
192	,,	23	,, ,,		1						4	4									11	3
221	,,	24	River Camel (Estuary)								1	1										+
222	,,	24	,, ,, ,,									1										
224	,,	24	Mevagissey Bay				1															
227	,,	24	,, ,,							1				2		1					+	+
237	,,	26	River Lynher			1									1							
238	,,	26	,, ,,	4																		+
241	,,	29	River Tamar												3							31
242	December	5	River Tamar (Estuary)									1										
243	,,	5	,, ,, ,,											2			9					
244	,,	5	,, ,, ,,					1														
245	,,	5	,, ,, ,,											2								
	1933																					
248	January	12	River Lynher	4											+							+
249	,,	23	Sutton Harbour (Plymouth)										4									
251			River Lynher								26	1	6	1	7						+	4
Total number of birds in which present				3	1	2	1	1	1	3	3	7	3	4	4	1	1	4	1	2	4	9
Total number of fish recognisable in birds examined				9	1	2	1	1	5	4	31	17	11	7	12	1	9	6	1	2	15	44

+ signifies "present."

River Lynher on January 5th, 1933, had unidentifiable flatfish fragments in its stomach.

The accompanying diagram, Figure 1, shows the approximate percentage numerical composition of the total food eaten by the Shags examined—excluding Clupeoid Britt and a few Crustacea. A single glance at this diagram will immediately reveal how insignificant is the number of flatfish and other food-fishes which enter into the diet of Shags and how largely these birds depend upon Sand Eels and other non-marketable species for their sustenance. During periods of stormy weather, however, some of them are often compelled to forsake their normal feeding-grounds and driven to seek their prey in the more sheltered waters of harbours and river estuaries where they occasionally devour flatfish. But even in these circumstances they do not appear to do so if they can find other food. Eleven birds driven inland in this way have been shot and found to contain recognisable food, but only three of them had any trace of flatfish in their stomachs. The very last Shag examined was shot in the River Lynher at the same time and in the same place as a Cormorant. The two birds had obviously been feeding together, for both their stomachs contained many Gobies—the Shag 35 and the Cormorant 26 of them. But whereas the Shag's stomach contained only Gobies the Cormorant had eaten in addition no less than 15 small flatfish.*

IV. Food of Cormorants (*Phalacrocorax carbo carbo* (L.)).

Twenty-nine Cormorants have been secured in the course of this investigation.† Twenty-seven of them contained recognisable food, the examination of which has yielded very definite and interesting results quite different from those obtained from the Shags. In Table III these results are shown in detail for each bird.

From this table it will be seen that 16 out of the 27 birds containing food material have been obtained from river estuaries as the result of the special efforts made to secure birds from such localities. Of these no less than 14 birds were found to have eaten one or more flatfish. It is clear, therefore, that flatfish form a large proportion of the food of Cormorants when they are feeding in the shallow waters of estuaries or harbours, which are their normal hunting-grounds. When foraging farther at sea, as they occasionally do, Cormorants devour the same kinds of fishes as Shags—with the exception of Sand Eels, which they appear seldom to capture; at any rate, not one of all the Cormorants examined had any trace of a Sand Eel in its stomach.

Figure 2 shows in graphic form the percentage numerical proportions of marketable and non-marketable fishes eaten by all the Cormorants examined in the course of this investigation. Flatfish formed nearly 40 per cent of the total. Other marketable species, including Clupeoids, formed roughly 10 per cent of the fishes devoured by them. Thus *very nearly half of the fishes eaten by these birds were marketable species of greater or less value.*

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* See Table III.

† See p. 280.

V. Discussion of Results.

Because of their habit of frequenting harbours and river estuaries Cormorants are observed hunting their prey much more frequently than are Shags. There is therefore little doubt that the complaints which from time to time have been made by Cornish fishermen concerning the killing of marketable fishes, and flatfishes in particular, by Shags and Cormorants have been based almost entirely upon observations of the depredations of Cormorants alone. A grave and expensive mistake was made, therefore, in considering Shags

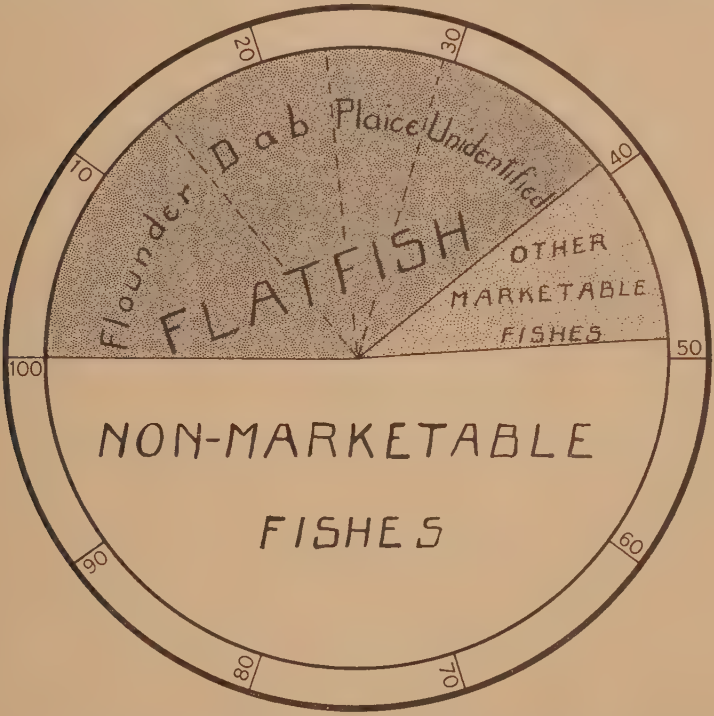

Fig. 2.—Diagrammatic representation of the percentage numerical composition of the food of Cormorants (Crustaceans omitted).

equally destructive. This error arose probably because Shags and Cormorants are very similar in appearance, and fishermen do not as a rule trouble to distinguish between them. It is just possible, however, that the published results of previous workers (applicable to other localities but not to this) had reached the fishermen or their Committee and helped to produce or confirm this erroneous belief. Witherby (**3**, p. 403), for example, states that the food of the Shag consists almost entirely of sea fish such as Plaice, Sillock, Wrasse, Eels (up to 2 ft. long), Herring, Garfish, Father-lasher, etc., and exceptionally also of crustacea and mollusca (Mytilus). Collinge (**1**, p. 220) examined the stomachs of 28 Shags,* 26 of which contained food material. He found that " excepting for a small percentage† (2·55) of crustacean remains and 1 per cent of algæ, the whole of the stomachs were filled with fish, cod, haddock, and whiting being easily identified." In a table (*op. cit.*, p. 221) showing the " monthly percentages of the principal food items of the adult Shag " the diet is recorded as varying between a maximum of 100 per cent food-fishes in November, December, and January and a minimum of 90·50 per cent in June, with an average of 96·45 per cent of food fishes over the whole year. These results are completely at variance with those obtained in the present investigation. The explanation of this disagreement may be that the staple food of Shags varies greatly in different localities, according to the different kinds of food organisms available. Haddocks, for example, are rarely found in this area, so they cannot form any part of the diet of sea-birds in Cornish waters.

With regard to the food of Cormorants, the statements of Witherby (*op. cit.*, p. 400) and Collinge (*op. cit.*, p. 218) and the results of this investigation are more in agreement. Witherby states that their diet consists almost entirely of fish, both fresh and salt water, including Trout, Eel, Pike, Flounder, Plaice, Sand-launce, 15-spined Stickleback, Haddock, young of Coal-fish, Mullet, and Conger (up to 2½ ft.), and that crustacea (including crabs and Pandalus) are occasionally taken. The absence of fresh-water fishes from the food of the birds examined in the course of the present investigation is due to the fact that no birds were obtained or sought from purely fresh-water feeding grounds.

As the result of the examination of 43 Cormorants with full stomachs, Collinge found that their largest food item consisted of food-fishes—95·80 per cent. Where identifiable they were found to be Cod, Haddock, and Whiting. Crustacean remains, believed by the author to be derived from the stomachs of the fishes eaten,‡ were found in 4 stomachs and represented 0·75 per cent of the total food. Miscellaneous unidentifiable matter amounting to 2·31 per cent, and 1·14 per cent of algæ were also found. Collinge therefore concludes that "if we regard a bird that feeds upon food-fishes as injurious, then there is nothing to be said in favour of the Cormorant." The evidence obtained in this area does not wholly support this downright condemnation of the birds. Around the shores of Cornwall Cormorants feed to no inconsiderable extent upon non-marketable species as well as food fishes.

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* Presumably obtained from various parts of the country, although no details are given.

† See footnote, p. 292.

‡ Several of the stomachs examined by the present writer contained Shrimps, Prawns, etc., which could not possibly have been derived from the stomachs of fishes eaten.

Perhaps the most striking difference between the food of the Cormorants examined by Collinge and those at present under discussion is the very much greater range of fish species which had been eaten by the latter (*vide* Table III, p. 284).

As Cormorants are observed hunting their prey much more frequently than are Shags, a false impression of the magnitude of the Cormorant population—and therefore of the damage that they do*—is likely to be acquired. It is necessary to point out, therefore, that Cormorants are much less numerous than Shags in both Devon and Cornwall. My colleague, Mr. G. M. Spooner, M.A., an active member of the Devon Bird-watching and Preservation Society, informs me that in South Devon, between Plymouth and Start Point, a careful census has shown that Shags are roughly 10 times as numerous as Cormorants. Although no actual census of the Shag and Cormorant populations in Cornwall has been made, it seems probable that the proportion of Cormorants in that county is even smaller than in Devon. In the whole of Cornwall (excluding the Scilly Isles) there are probably not more than one thousand Cormorants as compared with from 10 to 15 thousand Shags.

VI. ACKNOWLEDGMENTS.

I have much pleasure in recording indebtedness to my colleagues, Messrs. E. Ford and G. M. Spooner, for coming to my aid on several occasions when pressure of work made it difficult for me to deal expeditiously with consignments of birds.

VII. SUMMARY.

1. 188 Shags and 27 Cormorants, which had been feeding around the shores of Cornwall and whose stomachs contained identifiable food organisms, have been examined.

2. The Shags were found to have been feeding principally upon Sand Eels (Ammodytes spp.), and other non-marketable fishes.

3. The proportion of flatfishes and other economic species which had been devoured by the Shags was negligible.

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* Still another factor operates to convey an exaggerated impression of their depredations among flatfish. Because of their shape, flats are difficult fishes to swallow. A bird's efforts to dispose of a large individual, therefore, often attracts the attention of onlookers, whereas ordinary round fishes are swallowed too quickly and easily to be seen and recognised except on very rare occasions.

4. During the winter months Clupeoids (Sprats, Anchovies, etc.) were included in their diet.

5. The Cormorants had been feeding largely upon flatfish and other estuarine food-fishes.

6. Cormorants, which are frequenters of more or less enclosed waters, are much less numerous than Shags in both Cornwall and Devon.

VIII. LITERATURE CITED.

1. Collinge, W. E. The Food of Some British Wild Birds, 2nd edition. York, 1924–27.

2. Cornwall Sea Fisheries Committee: Minutes of Meetings. (*a*) 30th August, 1911; (*b*) 29th November, 1911; (*c*) 29th May, 1912; (*d*) 27th August, 1913; (*e*) 26th May, 1915; (*f*) 24th November, 1915; (*g*) 30th May, 1923; (*h*) 23rd September, 1925; (*j*) 18th December, 1929.

3. Witherby, H. F. A Practical Handbook of British Birds, Vol. II. London, 1924.

IX. APPENDIX I.

As the food consumed by Shags and Cormorants in this area has been found to differ greatly in important respects, it will be useful here to tabulate the main features by which these birds are distinguished.

Cormorant.	Shag.
1. Body plumage bronze-brown and black (winter and summer).	Body plumage greenish black, the green gloss being less pronounced in winter than in summer but always present.
2. Sides of head and chin brownish white (colour produced by white feathers tipped with brown); in summer, pure white, the feathers having no brown edges.	Chin and round base of lower mandible only, may have varying amounts of white to brownish white; in summer, whole of chin and throat glossy green without any trace of white or brown.
3. In summer, large patch of white feathers at base of thigh.	Never has any white on thigh.
4. Has 14 tail feathers.*	Has 12 tail feathers.*
5. Overall length of adult bird usually between 33 and 38 inches.	Overall length of adult bird usually between 25 and 30 inches.
6. Weight of adult bird usually between 5½ and 8½ pounds.	Weight of adult bird usually between 3½ and 5 pounds.
7. Frequents harbours, estuaries, and tidal rivers, or even inland lochs and reservoirs.	Entirely marine, frequenting open, exposed, and usually rocky sea-coasts. Occasionally is found feeding in sheltered waters when driven in from its usual haunts by stormy weather.

* These numbers are not absolutely constant.

In the field the Shag can be distinguished from the Cormorant by its noticeably smaller size, greenish black plumage, and smaller amount of white around the chin and neck. In breeding dress the Cormorant can readily be identified by the conspicuous patch of white feathers at the base of the thigh.

The immature birds are less easy to distinguish except by size. The breast and abdomen of the young Cormorant may, however, be dull white mottled with brown. The breast of the immature Shag is never white.

The Cormorant swims with its bill pointed upwards and when diving usually submerges its head and glides under water with scarcely a ripple. The Shag, on the other hand, often springs quite clear of the water in diving.*

X. APPENDIX II.

Collinge (*op. cit.*, p. 31) expresses the hope that in all future investigations into the food of wild birds the " volumetric or percentage by bulk " method of recording the stomach contents will be employed rather than any of the various modifications of the numerical system.† He urges the adoption of the former method because he is convinced of "its superiority and greater scientific accuracy over any other."

In the opinion of the present writer this conviction can be justified only when applied to the stomach contents of birds whose food consists of vegetable products either wholly or in part, and where the economic values of both plant and animal food materials have to be assessed and balanced against each other. According to Collinge (*op. cit.*, p. 27), however, " if we say that a bird's stomach contains sixty aphids and six bees the idea furnished is a ratio of 60 to 6, but if computed by the percentage of bulk the ratio would be more correctly stated by the figures 3 to 28 of the total food contents of the stomach," and this author believes the second expression to be much the more valuable for the purpose of assessing the usefulness or otherwise of the bird in question. In reaching this conclusion he has failed to take into consideration the fact that the sizes of organisms seldom or never bear any relation to their activities, whether beneficial or harmful, or to their marketable value, either actual or potential. In the present investigation, for example, one Cormorant was found to have eaten 15 small flatfishes between 5 and 10 cm. in length. The combined volume of all these fishes was less than that of a single fully grown adult. But they would have produced 15 adult marketable fishes had they been allowed to live. By destroying these young individuals, therefore, this particular bird had done quite as much *potential* harm to the fish stock as if it had eaten an equal number—*or over 20 times the volume*—of adults.

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* See also Witherby's " Handbook."

† See p. 280.

A further criticism levelled against the numerical method is that it cannot successfully be applied to finely comminuted animal or vegetable matter (**1**, p. 29). In my experience this applies also to the volumetric method, at any rate when dealing with fish-eating birds. Fragmentary food remains which are so far disintegrated as to make it impossible to ascertain from how many individuals they were derived are seldom or never in such a state that they can be accurately identified. To determine their volume, therefore, even when this may be possible with any degree of accuracy,* would add but little to the value of the record.

Again, a bird whose stomach contained, say, three tails of *Gobius flavescens* would, in the numerical computation, be recorded—and accurately so—as having eaten three of these fish. By volumetric computation, if the stomach contained any other food, the proportion of Goby would work out at considerably less than would have been produced by a single whole individual. If, however, no food were present, the percentage proportion by bulk would have to be recorded as 100 *per cent Goby* whether the stomach contained only one recognisable fragment or whether it was packed with a large number of the fish. A " volumetric " or " proportion by bulk " expression of the results in such instances can have no real meaning. Moreover, if such separate readings be taken into consideration when calculating the proportions of the total food eaten by all the birds examined they will produce, or tend to produce, totally false final values. If, on the other hand, in order to eliminate this grave source of error, all stomachs containing only one kind of food organism are disregarded, the final computations will be equally unreliable and misleading.

Ideally, of course, a combination of all possible methods of exact computation is desirable. In the present investigation this would have been quite impracticable. What was believed to be the most satisfactory of the various methods available was therefore chosen.

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* The accuracy obtainable is never such as to justify expressing the results correct to two places of decimals (see p. 288).

The Magnesium and other Inorganic Constituents of some Marine Invertebrates.

By

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With 1 Figure in the Text.

THE livers of some of the marine invertebrates are well known to contain unusually high concentrations of certain of the heavy metals, such as iron, which are normally found in smaller amounts throughout the animal kingdom. Other invertebrate animals contain relatively high concentrations of metals which are not usually found, or only in the merest traces, in the higher animals. The present paper describes what is believed to be a new observation not quite falling into either category.

In the course of some work on the organic and inorganic constituents of food the following marine invertebrates were subjected to analysis: Oysters (*Ostrea edulis*), Scallops (*Pecten maximus*), Winkles (*Littorina littorea*), Mussels (*Mytilus edulis*), and Whelks (*Buccinum undatum*). These were all analysed cooked, except the Mussels and Oysters, and nothing very striking was observed in their inorganic 'make up' except in the case of the Winkles and the Whelks. These animals were found to contain 414 and 160 mg. of magnesium respectively per 100 g. of wet cooked flesh. These figures are the mean of several analyses. In mammals, birds and fish the magnesium was found to lie between 10 and 35 mg. per 100 g. of live weight and to vary to some extent with the organ. Muscular tissue, for example, contained 22 to 35 mg. per 100 g. and mammalian kidney 16 mg. per 100 g., while eggs and fish roes (male and female) contained only 10 mg. per 100 g. The $\frac{\text{Na}}{\text{Mg}}$ ratios in fish and mammalian muscle lay between $\frac{3}{1}$ and $\frac{5\cdot5}{1}$.

The detection of these abnormal magnesium concentrations in the winkles and the whelks was considered of sufficient biological interest to warrant further investigation. With the assistance of the Director and Members of the Marine Biological Association's Laboratory at Plymouth, *Cardium edule*, *Pecten maximus*, and *Littorina littorea* were obtained in the raw state and the individual organs analysed. Water, sodium, potassium, calcium, magnesium and iron were determined. A complete survey of the methods used is in course of publication. (McCance & Shipp, 1933.) A brief note on the magnesium technique is, however, necessary. After incineration of the material and extraction with hydrochloric acid the solution was neutralised to phenol red, made just acid with acetic acid and the calcium removed as the oxalate. The magnesium was precipitated from the calcium free solution as magnesium ammonium phosphate, and the phosphate in the precipitate determined by Brigg's (1922) method.

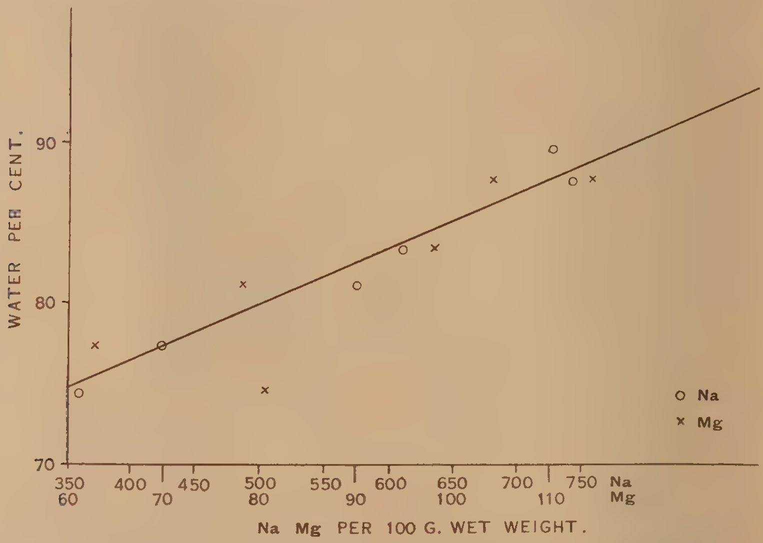

FIG. 1.—The relation between the water and the sodium-magnesium contents of the organs of *Pecten maximus.*

To ensure that the whole of the phosphate was present as the magnesium salt and not in combination with some quite unexpected metal, a large amount of the precipitate from the winkles was collected and weighed after ignition to the pyrophosphate. The weight of phosphate in the ignited salt corresponded with the theoretical amount required for magnesium pyrophosphate, and no metal other than magnesium was found when the precipitate was dissolved and subjected to qualitative analysis.

The results obtained may be found in Table I (p. 296).

The points to which we wish to draw attention are :—

(1) The very high concentration of magnesium in *Littorina littorea.* The $\frac{\text{Na}}{\text{Mg}}$ ratio in these animals is approximately $\frac{1}{1}$. The element appears to

be distributed throughout all the organs in amounts which would be fatal to higher animals. The physiological significance of this is at present quite obscure.

(2) The high but rather variable magnesium in the different organs of Cardium and Pecten. In Pecten $\frac{\text{Na}}{\text{Mg}}$ is roughly $\frac{6{\cdot}5}{1}$ and in Cardium $\frac{4{\cdot}3}{1}$. It will be observed that the magnesium, sodium and water tend to vary together. The relationship in Pecten is demonstrated by Figure 1.

(3) The low concentration of magnesium in mussels and oysters. The $\frac{\text{Na}}{\text{Mg}}$ ratios are about $\frac{14}{1}$.

(4) The potassium concentration in the various organs of these invertebrates runs parallel not with the water but with the dry matter. The potassium, as might have been expected, seems to form an integral part of the protoplasm and only small variations are compatible with life.

(5) The variations in iron from one animal to another and from one organ to another are striking and their importance unknown.

SUMMARY.

The sodium, potassium, calcium, magnesium and iron of a number of marine invertebrates have been determined and some of the findings are very briefly discussed.

The common winkle *Littorina littorea* contains 330–510 mg. of magnesium per 100 g. of live weight. All the organs appear to contain these high concentrations. Boiled specimens of whelks contained about 160 mg. of magnesium per 100 g.

We should like to thank the Director and Staff of the Laboratory of the Marine Biological Association for their assistance. R. A. McC. has held a part-time grant and H. L. S. a full time grant from the Medical Research Council during this work.

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TABLE I

Animal.	Organ.	Water %	Na.	K.	Ca.	Mg.	Fe.
			mg. per 100 g. of live wet weight.				
Mytilus edulis	Whole		290	315	90	23	5·8
Ostrea edulis	Whole		650	258	185	41	6·0
Littorina littorea	Foot	64·6	425	375	265	346	17·8
	Mantle	70·9	415	277	1266	334	18·7
	Gonad	65·2	342	390	168	460	26·8
	Stomach and Liver	67·7	438	473	550	507	33·6
Pecten maximus	Foot	83·6	612	250	42	97	2·8
	Mantle	87·9	742	148	52	104	0·9
	Muscle	77·4	424	387	26	63	1·8
	Gonad	81·1	566	283	38	78	5·8
	Gills	89·8	726	143	54	111	1·7
	Stomach	74·4	351	262	118	80	11·2
Cardium edule	Foot	77·4	510	305	41	93	15·5
	Mantle	84·5	610	180	180	117	17·5
	Muscle	73·5	482	300	70	84	3·9
	Gills	83·5	294	239	87	106	7·3
	Stomach, Liver, etc.	71·1	241	302	145	94	8·1

Abnormal Eyes in Wild *Gammarus zaddachi* Sexton.

By

R. Bassindale, M.Sc.

With 2 Figures in the Text.

During the course of a biological survey of the Tay Estuary collections of the species of Amphipoda found in the tidal zone were made from Bridge of Earn, near the limit of tidal waters in the River Earn, down to the confluence of the Rivers Earn and Tay, and thence to Tayport, near the sea. Between Newburgh and Bridge of Earn (from 23 to 32 miles from the sea) the only Amphipoda recorded were 198 specimens of Gammarus and one specimen of *Melita palmata* (Mont.). The water in this part of the Estuary, although tidal, is for the most part fresh, attaining at Newburgh at high tide an average salinity of only 3 or 4 gm. per 1000 gm.

Four collecting stations were investigated in the zone described and all the Gammarus were identified by Mrs. Sexton as *G. zaddachi* Sexton, a brackish-water species described by Mrs. Sexton herself (**1**). Of these 198 specimens, four were observed to have abnormal eyes. Although this condition has been previously described from a Laboratory strain of *G. chevreuxi* (**2**) this is the first occasion on which wild specimens have been recorded with similar abnormalities.

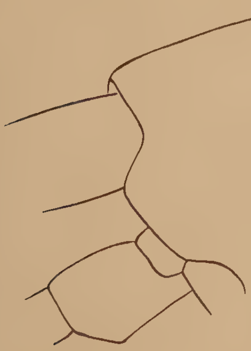

Fig. 1.

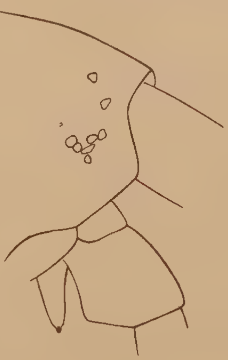

Fig. 2.

Of the four individuals, No. 1 was taken at the highest station at Bridge of Earn, and No. 2 was found at the second station some 3 miles lower down the Estuary. Nos. 3 and 4 both occurred at Newburgh, the lowest station at which *G. zaddachi* was found.

Specimen No. 1 is small, measuring about 5 mm. along the dorsal line. Both eyes are irregular, the left being rounded instead of reniform with the margin indented : the right eye is roughly triangular, very similar in shape to the one figured by Sexton (**2**) (Text-fig. 7, p. 356).

Specimen No. 2 is slightly larger (*ca* 7½ mm.) and is remarkable in having only one eye developed—on the right side—practically normal in size and shape. There is no trace of an eye on the left side (Fig. 1).

Specimen No. 3 is the largest (15 mm.) and has suffered damage after capture. The eyes, however, show distinct irregularities in size (the right being much smaller than the left), in shape and in the arrangement of the ommatidea.

Specimen No. 4 (6½ mm.). The head is much narrower in proportion to the body measurements than in the normal animal. The right eye is degenerate, closely resembling the albino mutation of *G. chevreuxi*, and consists of a few scattered colourless cones (Fig. 2). The left eye was evidently large and pigmented in life, but has suffered damage and the exact details cannot be determined.

SUMMARY.

Of 198 specimens of *Gammarus zaddachi* collected in the Estuaries of the Rivers Earn and Tay four individuals had abnormal eyes. This is the first record of abnormal eyes in wild specimens of a Gammarus species, although Laboratory strains of *G. chevreuxi* have developed them.

The investigation described in this paper was carried out as part of the programme of the Water Pollution Research Board of the Department of Scientific and Industrial Research, and is published by permission of the Department. My thanks are due to Dr. E. J. Allen and to Mrs. E. W. Sexton for their assistance in preparing the paper.

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2. Sexton, E. W. Degeneration and loss of the eye in the Amphipod *Gammarus chevreuxi* Sexton, Part I. Journ. Mar. Biol. Assoc., N.S., Vol. XVIII, No. 1, 1932, p. 355.

Notes on Some Copepoda from Plymouth.

By

Robert Gurney.

With 4 Figures in the Text.

Tisbe elongata A. SCOTT. HARPACTICID INHABITING THE GILL CHAMBER OF THE LOBSTER.

WHEN examining the gills of a lobster for specimens of Nicothoe large numbers of copepods were found which, colourless and slender in form, had the sluggish and rather aimless movements which one would expect from a commensal removed from its natural habitat. It was somewhat of a surprise to find that they all belonged to a species already described —*Tisbe elongata* A. Scott. Scott obtained a few specimens from mud collected on mussel beds between Heysham and Morecambe. It appears, then, that we have here a species which is capable of free life, but its abundance, in all stages of growth, in the gill chamber of a lobster, proves that it is also to be considered a semi-parasite.

The occurrence is of some interest, as examples of parasitism are rare among Harpacticids. The closest parallel is the record of Kröyer of *Machairopus hippolytes* (Kröyer) in the gill chamber of *Spirontocaris grœnlandica* Fabr. Hansen* supposed that this occurrence was accidental; but it is probable that this is also a case of semi-parasitism.

Aurivillius has recorded the finding of *Tisbe furcata* in the Ascidian *Molgula ampulloides*, but this was no doubt simply accidental, as *T. furcata* is a ubiquitous littoral species. The only Harpacticid actually becoming a fixed and more or less degenerate parasite is also a member of the Tisbidæ—*Cholidya polypi* Farran parasitic on Octopus. Other more or less parasitic species are :—

Balœnophilus unisetis Aurivillius, on Whales. *Sunaristes paguri* Hesse, in shells of Hermit Crabs. *Cancrincola jamaicensis* Wilson, on gills of the crab Cardisoma. *Cancrincola wilsoni* Pearse, on gills of the crab Sesarma. *Nitocrameira bdelluræ* Liddell, on gills of Limulus. *Nitocra divaricata* Chappuis, on gills of Potamobius. *Tisbe wilsoni* Seiwell, in the Ascidian Amaroucium.

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* 1923, *Ingolf Exped.*, iii, p. 74.

LARVAL STAGES OF *Misophria pallida* BOECK.

The systematic position of Misophria is still a matter of complete uncertainty, and it was to be expected that its nauplius, if it could be found, might throw light on the subject. At Plymouth *M. pallida* is extremely difficult to obtain, but can be found by diligent search of dredgings from the Sound. During two visits, however, none were to be found with eggs, and it was only on the third attempt, in July 1932, that egg-bearing females were taken and the eggs successfully hatched.

The female bears 2–4 large eggs, loosely attached to the genital somite, but not, apparently, enclosed in a definite egg-sac, and the eggs seem to be carried for a considerable time before hatching. Unfortunately the nauplius, after all, provides no definite evidence for the systematic position of the adult. It is without eye or mouth, the body filled with yellow yolk, and the appendages naturally without any masticatory processes (Fig. 1). The antennæ and mandibles are large, with 4-segmented exopods, and beneath the cuticle can be seen rudiments of legs 1 and 2. Within about a day it moults to the 1st copepodid stage which has the same habit as the adult of gliding movement on the bottom. The appendages, though not fully developed, are quite of the adult plan (Fig. 2).

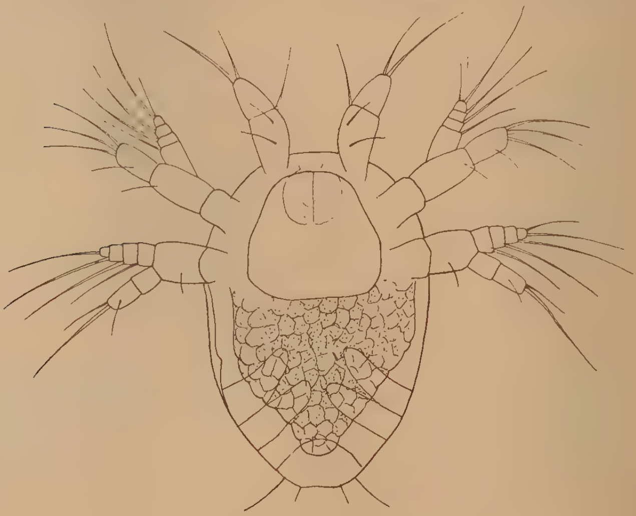

FIG. 1.—Nauplius of *Misophria pallida*.

What is of interest in this life-history is the almost complete cutting out of the nauplius stages. No Calanoid and no Harpacticid is known with a yolk-filled egg of this type and a non-feeding nauplius, a point which may be regarded as some evidence against relation to either of these groups. Among the Cyclopoida also nothing of the kind is known, except among the semi-parasites such as the Ascomyzontidæ, and there cannot be any question of any relation to them. The nauplius may be said to resemble much more closely the Cyclopoid type than that of the Calanoids, and to be quite unlike that of such Harpacticids as are known, and to

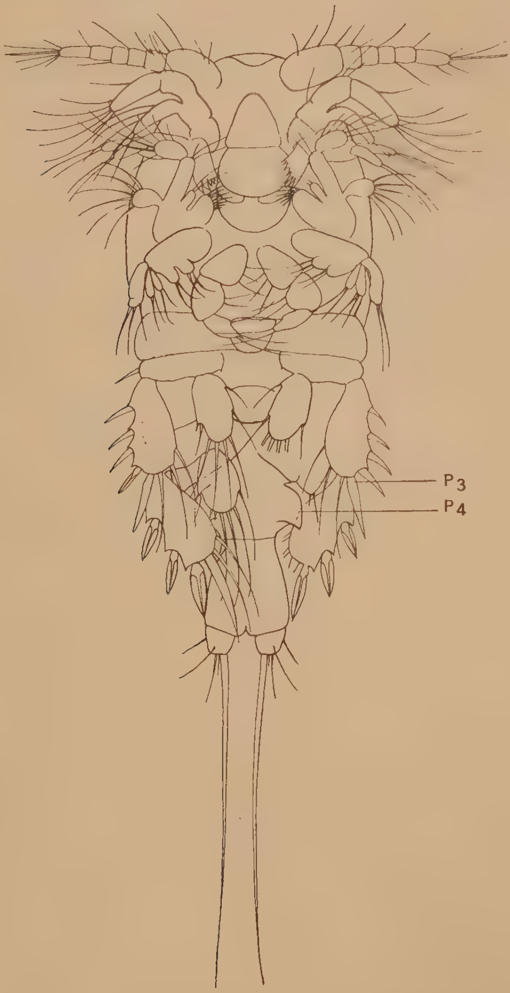

Fig. 2.—*Misophria pallida*, first Copepodid stage.

this very small extent relation to the Cyclopoida is suggested. The copepodid provides no useful evidence. The same plan in stage I is universal among Copepods, and the appendages already have the characters of the adult. If any conclusion can be drawn from the meagre facts, it seems to be that, in its larval history, as in its adult structure, Misophria holds an isolated place, which can best be expressed by regarding it as the type of a separate Order Misophrioida.

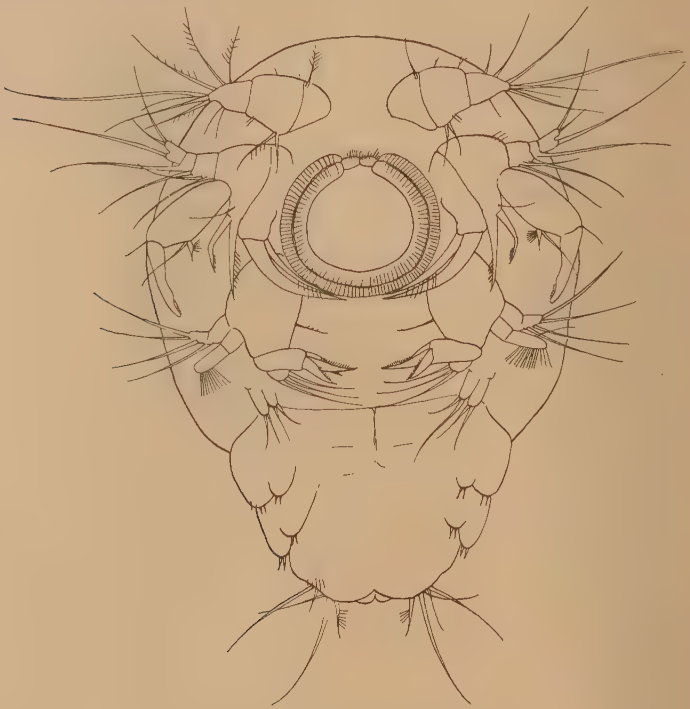

FIG. 3.—Nauplius of *Psamathe longicauda*.

THE NAUPLIUS OF *Psamathe longicauda* PHILIPPI.

Among a number of littoral Harpacticids handed over to me by Mr. John Colman were some nauplii of *Psamathe longicauda* which proved to have a structure of unusual interest (Fig. 3). This nauplius has already been described by Brian,* but without drawing special attention to the particular point of importance, which is the modification of the whole of the upper lip into a sucker. The upper lip is a hollowed circular disc the margins of which are strengthened by radial chitinous rods and fringed with very delicate hairs (Fig. 4). Anteriorly there is a gap in the disc which is closed by a pair of hairy pads. This sucking disc persists through the nauplius stages, but is lost at the moult to the copepodid, in which the upper lip is not modified. So far as I know a sucker of this kind is quite unknown in all other Harpacticids. In the closely allied *Aspidiscus littoralis* there is nothing of the kind, but in this case the margin of the dorsal shield has a delicate hyaline membrane which may serve to convert the whole body into a sort of sucker. On the other hand, suckers of strikingly similar form are found on the maxillæ of the Branchiura, which are not Copepods at all, on the anterior margin of the head in some Caligidæ, and in a number of parasitic forms at the apex of the mouth cone. In this last case, however, the sucking disc is largely, or wholly, the product of the modified lower lip, and the mandibles are enclosed in the mouth cone. The closest parallel to the disc of Psamathe seems to be found in Eunicicola. According to the figures given by Sars of *E. clausi* the disc is here, as in Psamathe, entirely formed by the upper lip, and the mandible, if it exists, is behind it. It is therefore simply an organ of adhesion and not, as in Lernæopods, for example, a sucking disc for feeding purposes.

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* *I copepodi Harpacticoidi del Golfo di Genova*, 1921, p. 25.

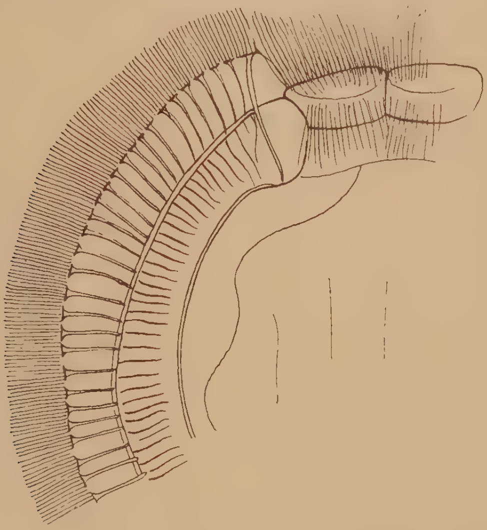

FIG. 4.—Structure of the Sucker of *Psamathe longicauda*.

THE NAUPLIUS OF NOTODELPHYS.

In his description of the nauplii of *Notodelphys agilis* and *Doropygus porcicauda** Mr. Peter Gray draws special attention to the absence of an endopod from the mandible, which he claims to be otherwise unknown among nauplii. This is not altogether true, since an uniramous mandible is found in certain Branchiopod nauplii, but it is a remarkable feature in a Copepod. On the other hand Canu, in 1892,* gave excellent figures of the nauplii of *Notodelphys agilis* and of *Doropygus gibber*, and in both cases showed a small endopod on the mandible. I have myself seen the nauplius of *N. allmani*, and in this species (which is also figured by Canu) the endopod is quite distinct. A difference between the two species *D. porcicauda* and *D. gibber* in this respect is not impossible, but seems most unlikely, in view of the fact that an endopod is present in all the nauplii of Notodelphyids described by Canu—*Bonnierella longipes*, *Doroixys uncinata*, *Enterocola fulgens*, *Aplostoma brevicauda*, besides those mentioned above.

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* *Journ. Mar. Biol. Assoc.*, xviii, p. 519, 1933.

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* *Trav. Lab. Zool. Wimereux*, vi, 1892.

An Account of the Herring Investigations Conducted at Plymouth during the Years from 1924 to 1933.

By

E. Ford, A.R.C.Sc.,

Fisheries Naturalist at the Plymouth Laboratory.

With a Chart and 10 Figures in the Text.

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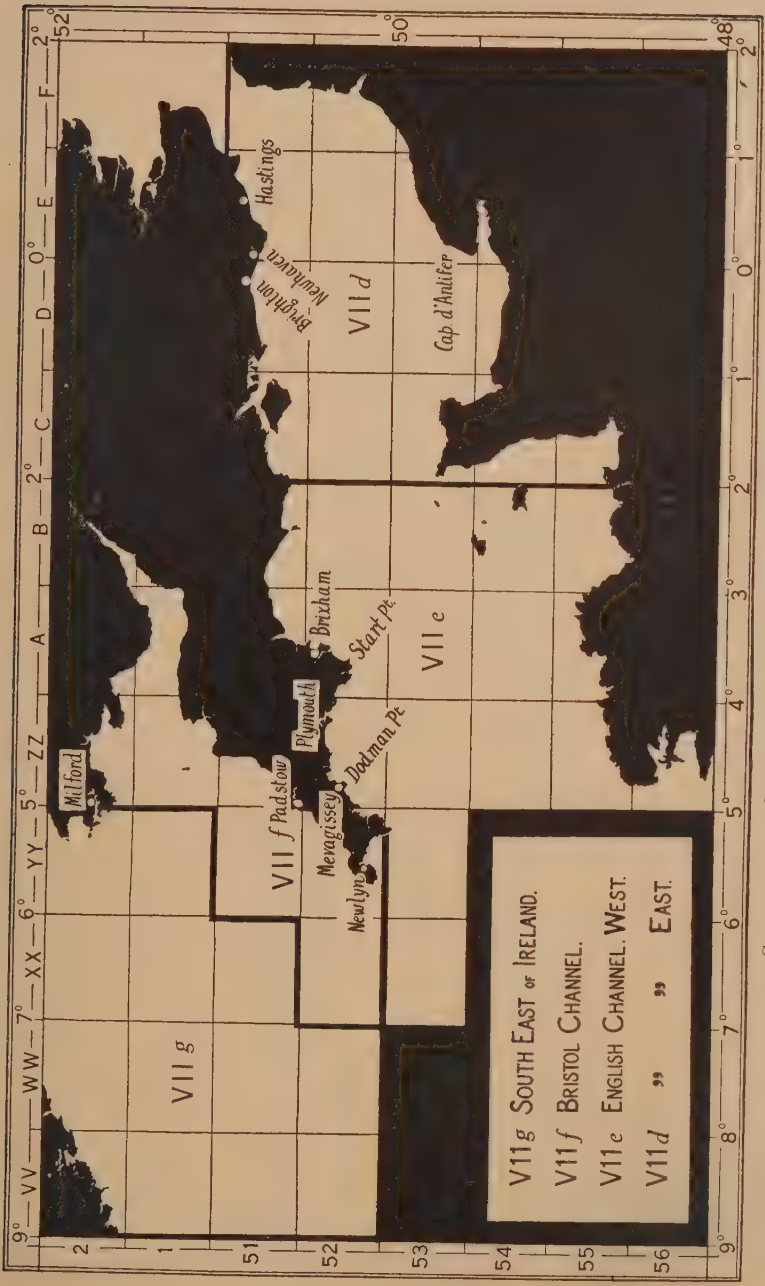
INTRODUCTION.

THE Plymouth Laboratory is well situated for the study of the herring and its commercial fishery, and since the winter of 1924–25, advantage has been taken of the varied facilities for research thus afforded. From time to time reports have been published in the Journal of the Marine Biological Association as a series, entitled : "Herring Investigations at Plymouth" and these have dealt with many seemingly distinct subjects of study, including experiments with larvæ from laboratory-fertilised eggs ; studies of growth, migration and structure of young and old fish ; and accounts of the commercial operations during the winter drift-fishery at Plymouth. It has now been considered advisable to bring together the several results in one paper, in an endeavour to show their essential bearing upon the problems of the practical fishery.

The first part of the paper is a descriptive account of the actual winter fishery at Plymouth which is of sufficient commercial importance to warrant the collection of information on the essentially business matters of catching, landing and marketing. This fishery, however, no less than any other drift-net fishery, is perforce conducted under difficult conditions of uncertainty. Fishermen and merchants alike are only too well aware of the extent to which the yield is liable to fluctuate from day to day and from season to season, and their business operations are rendered even more difficult because they can neither foresee nor prepare for the circumstances, favourable or otherwise, which each new season holds in store. It will not be questioned, therefore, that if scientific enquiry can ultimately succeed in removing this uncertainty from the fishery, it will have accomplished an essentially practical service. But it may be stated with equal assurance that this practical end can only be attained through a very exhaustive study of the life-history, habits and migration of the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Milford
Hastings
Newhaven
Brighton
VII d
Cap. d'Antifer
Brixham
Start Pt.
VII e
Plymouth
Padstow
VII f
Dodman Pt.
Mevagissey
Newlyn
VII g
V11g South East of Ireland.
V11f Bristol Channel.
V11e English Channel. West.
V11d ,, ,, East.

Chart showing Statistical Regions dealt with in this Paper.

herring itself. And in this study the task of the investigator is made hard because so much of the needed information has to be sought for in an indirect way. The development of this indirect technique involves a great deal of preliminary research which at first sight appears to have but little bearing upon the practical fishery, but it is none the less essential. In the pages which follow, much of the text is devoted to the nature and application of such basic investigation, and an endeavour has been made to show how the different lines of enquiry meet in the central study of the fluctuations of the fishery. With so many distinct topics to be considered, it has not been found easy to preserve full continuity from section to section, although this has been done as far as possible. For the same reason it has been found impossible to avoid technical treatment in some instances, so that the general reader may find certain sections less easy to read than others. The paper concludes with a consideration of the question of forecasting the yield of the fishery from information gathered in preceding years.

THE PLYMOUTH WINTER DRIFT-NET FISHERY.

From November until the end of January, Sutton Harbour at Plymouth functions as the base for a large number of drifters which fish the neighbouring inshore waters for herrings. The season opens with the arrival of motor drifters from Cornish ports, but as soon as daily results prove sufficiently attractive (usually at the beginning of December) steamers from Lowestoft and Yarmouth augment the fleet. At the height of the season there may be between two and three hundred drifters at work. Circumstances permitting, they fish each night and land their catches in the morning. The steamers work continuously throughout the seven days of the week, but the Cornishmen do not land on Sundays.

Sutton Harbour and the adjoining fishmarket are the property of the Sutton Harbour Improvement Company, whose officers control the movement of vessels to and from the fish quay and supervise market proceedings. Catches are sold by public auction on the evidence of small samples exposed on a tray in front of the auctioneer's rostrum. Fishermen bring their samples and queue up in front of the rostrum awaiting their turn for a sale.

The herrings are bought chiefly to supply a fresh-fish market either at home or abroad. Home buyers arrange to have their barrels and boxes stacked alongside the quay, so that purchases can be swung out of the ship in quarter-cran baskets and shot direct into the containers in which they are to be forwarded to their destination. The quantity taken out of the ship is checked basket by basket, and ice is strewn over the fish as packing proceeds. When packed and labelled, the consignment is conveyed by lorry to the railhead at one of the Plymouth stations. Herrings bought by the "Klondyke" trade for export to the Continent are not unloaded at the quayside but conveyed direct to the carrier-vessel by the drifters themselves.

QUANTITY AND VALUE OF FISH LANDED.

The quantity and value of the fish landed at Plymouth vary from season to season and from day to day. The extent of these variations is considered below.

Seasonal Variation.

The Ministry of Agriculture and Fisheries collects statistics of the landings at Plymouth, and Table I shows the weight, value and average price of herrings landed during the months of December and January in the course of the past quarter of a century :—

TABLE I.

Season (Dec.–Jan.)	Total Weight Landed. Cwt.	Total Value. £		Average Price per 1 Cwt. s.	d.
1906–07	32,913	8,040		4	11
1907–08	23,957	6,583		5	6
1908–09	4,257	2,521		11	10
1909–10	52,544	16,105		6	1
1910–11	37,741	17,048		9	0
1911–12	39,167	18,158		9	3
1912–13	8,171	3,594		8	10
1913–14	28,886	13,933		9	8
1914–15	7,585	6,021		15	11
1915–16	11,582	13,062	War Period.	22	7
1916–17	24,293	35,901		29	6
1917–18	38,108	88,453		46	5
1918–19	8,624	15,160		35	2
1919–20	29,425	40,045		27	3
1920–21	40,263	42,752		21	3
1921–22	16,922	14,792		17	6
1922–23	54,839	26,326		9	8
1923–24	98,684	65,290		13	3
1924–25	113,585	109,294		19	3
1925–26	105,643	89,334		16	11
1926–27	63,138	47,539		15	1
1927–28	122,419	65,451		10	8
1928–29	75,104	44,475		11	10
1929–30	86,955	63,569		14	7
1930–31	94,811	52,973		11	2
1931–32	45,865 + 40 by trawl	37,620*		16	5
1932–33	79,532 + 499 by trawl	41,025*		10	3

The figures show that the yield varies considerably from season to season. Even so, greater quantities have been landed since the war than before it, and the seasonal average price is still above that of 1913–14.

* Value inclusive of trawled fish.

Daily Variation.

Information concerning daily variation in yield is obtainable from the daily returns of which the seasonal statistics given in Table I are the aggregate. It is found that there are many days in each season when the total weight of fish landed is comparatively small. For example, Table II is an analysis of daily statistics for the past five seasons :—

TABLE II.

Season (Dec. Jan.)	Total No. of Days.	No. of days on which landings were of the following weights (cwt.) Less than 1000	1000 to 1999	2000 to 2999	3000 to 3999	4000 to 4999	5000 to 5999	6000 to 6999	7000 to 7999	8000 to 8999	10000 to 10999	13000 to 13999
1928–29	54	35	6	4	3	3	–	1	–	2	–	–
1929–30	54	30	15	3	–	–	2	–	1	1	1	1
1930–31	60	31	10	6	6	4	3	–	–	–	–	–
1931–32	60	44	11	2	1	2	–	–	–	–	–	–
1932–33	56	33	11	2	5	2	1	–	1	–	1	–

It is seen that on considerably more than half the total number of days when landings were made, the amount landed was less than 1,000 cwt. Indeed, further analysis of statistics shows that the daily weight was actually less than 500 cwt. on 26, 21, 22, 34 and 26 days respectively, during the five seasons. This being so, it is hardly surprising that the comparatively occasional large daily landings should tend to sell at glut prices. The figures for 1929–30 provide a good illustration. During December and January, a total of 86,955 cwt. was landed. Of this amount, 36,502 cwt. was landed in 48 daily lots of less than 3,000 cwt., and sold for £41,351. This represents an average price of 22s. 8d. per 1 cwt. for approximately 42 per cent of the season's total catch. The remaining 58 per cent., or 50,453 cwt., was landed in 6 lots only and realised £22,218, representing an average price of 8s. 10d. Of these 6 lots, 3 were on the consecutive days, December 17th, 18th and 19th, when a total of no less than 30,900 cwt. was landed and sold at an average price of 6s. 4d.

A second illustration is provided by the statistics for the period, December 10th to 16th, 1928 :—

Date. 1928. Dec.	Weight Landed. Cwt.	Total Value. £	Price per 1 Cwt. s.	d.
10	222	564	50	10
11	7	10	28	7
12	1,465	1,465	20	0
13	8,050	4,600	11	5
14	8,050	2,926	7	3
15	6,030	1,785	5	11
16	3,875	1,525	7	10

From these two illustrations it is clear that only limited significance can be attached to the seasonable average price per 1 cwt., obtained by dividing the total value for the season by the total weight sold. This average tends to mask the relation which exists between the weight of fish landed in any one day and the price which it commands.

THE INTENSITY OF FISHING.

One of the causes of fluctuation in yield is that the intensity of fishing varies. The number of fishing vessels which participate in the fishery is not constant from season to season, and conditions of weather often seriously curtail the activities of those which do come. These and other factors affecting the intensity of fishing will now be considered.

Changes in Fishing Power.

The composition of the fishing fleet in each season since 1918–19 is shown in Table III, the data being supplied by Mr. W. G. Nelder, Manager of the Sutton Harbour Improvement Company, Plymouth :—

TABLE III.

Season.	Number of East Country Steamers.	Number of West Country (Cornish) Motor Drifters.	Number of Local Motor Drifters.
1918–19	33	139	Average No. is 10, some years only 3.
1919–20	30	156	
1920–21	26	182	
1921–22	31	155	
1922–23	68	142	
1923–24	59	161	
1924–25	86	176	
1925–26	153	158	
1926–27	129	169	
1927–28	77	145	25
1928–29	81	170	12
1929–30	54	169	12
1930–31	75	177	14
1931–32	52	170	20
1932–33	85	161	12

Dealing first with the motor drifters (mostly Cornish vessels), it is seen that the number has been well maintained throughout all the post-war years. During the fifteen seasons from 1918–19 to 1932–33, they landed an aggregate weight of 400,355 cwt. of herring as compared with the corresponding aggregate of 635,226 cwt. landed by the steamers. Taking into account the number of motor drifters in comparison with that of the steamers, it is estimated that the steam fishery has been from four to five times as efficient as the motor fleet, so far as weight per fishing unit is concerned.

The number of steamers has not been so steady. The large number of arrivals in 1925–26 and 1926–27, for example, is in marked contrast with those of the seasons from 1929–30 to 1931–32. It is of interest to enquire into the reasons for this irregularity in the number of steamers which form so important a section of the fishing power. Data show that there is a rise in the number of steamers in the season which follows one of good fishing. Thus, fishing was good in 1924–25 when 86 steamers came, and in the following season 153 steamers made the trip. Similarly, the good fishing of 1929–30 was followed by the arrival of a larger number of steamers in 1930–31. But the reverse seems to hold good, the number of steamers becoming reduced in the season following poor fishing. In 1925–26 fishing was bad, so that fewer steamers came in 1926–27. It was again poor, and the number of steamers was still less in 1927–28.

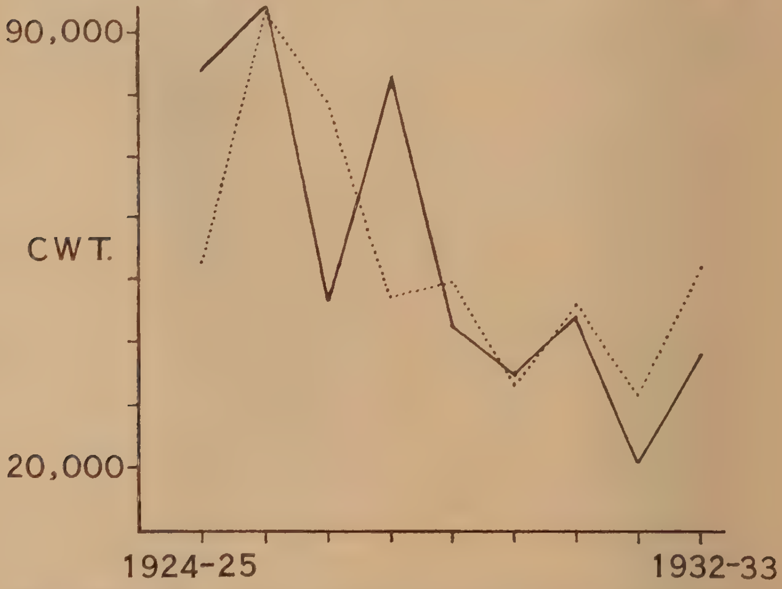

Fig. 1.—Total weight of herrings landed at Plymouth in each season from 1924–25 to 1932–33.

Continuous graph.....Actual weight landed.

Dotted graph........Hypothetical weight on basis of flat rate of 611 cwt. per steamer per season.

There are, of course, other influences which help to decide how many steamers will participate in the Plymouth fishery. The Plymouth season follows hard upon a strenuous and extended fishery in the North Sea, culminating in the great East Anglian season. Owners of steamers will know how they have fared thus far, and may or may not be prepared to carry an additional risk at Plymouth. In any event, they are unlikely to send the ships round before they receive some assurance by news from Plymouth that there is at least the chance of making a profitable voyage.

A matter of some practical importance is the extent to which the total weight of fish landed during a season is affected by changes in the number of visiting steamers. Out of the 1,035,581 cwt. of herrings landed during December and January from 1918–19 to 1932–33, the steamers obtained 635,226 cwt., or over 61 per cent. The latter amount represents the combined result of 1,039 separate steamer-visits, a single visit being the whole or some part of one season. Now if the aggregate weight of fish landed and the total number of steamer-visits had been equally distributed over the fifteen seasons, approximately 42,348 cwt. would have been landed each season as the result of 69 steamer-visits. One steamer-visit would thus have contributed about 611 cwt. to each season's catch. This "spread-over" average is admittedly only a rough estimate of a steamer's fishing efficiency, but it serves the purpose intended. In the following Table the theoretical weight as calculated on the basis of 611 cwt. per steamer-visit is shown in conjunction with the actual weight landed during the seasons from 1924–25 to 1932–33 :—

Season.	Number of Steamers.	Theoretical Weight Landed, on basis of 611 cwt. per Steamer. (Cwt.)	Actual Weight Landed. (Cwt.)	Discrepancy. Actual Weight is More by :	Less by :
1924–25	86	52,546	83,647	31,101	
1925–26	153	93,483	94,248	765	
1926–27	129	78,819	45,932		32,887
1927–28	77	47,047	82,803	35,756	
1928–29	81	49,491	42,177		7,314
1929–30	54	32,994	34,264	1,270	
1930–31	75	45,825	44,071		1,754
1931–32	52	31,772	20,927		10,845
1932–33	85	51,935	47,793		4,142

It is evident from the above Table and the graph in Fig. I, that although the total weight landed yearly is dependent upon the number of steamers engaged, the fluctuation in yield from season to season, is not wholly due to this. In some years, particularly 1924–25 and 1927–28, fishing was much more productive than a flat rate of fishing would indicate, while in others, notably 1926–27 and 1931–32, much less fish was landed than would be expected.

Number of Landings.

It is common knowledge that the number of drifters which proceed to sea is different from day to day. Compulsory stoppages on account of inclement weather, and voluntary cessations from fishing over week-ends and holidays, result in an appreciable loss of fishing time. The motor fishery is the greater sufferer in these respects and anything from 15 to 30 days in December and January in each year pass without a single motor landing. The steam fishery is more fortunate, for the days are rare when at least one steamer does not land. The greater regularity with which the steamers are able to operate is exemplified by the following statistics for the period, December 23rd, 1931, to January 19th, 1932 :—

Date 1931–32.	Steamer Landings.	Motor Landings.	
Dec. 23	20	90	
24	20	–	
25	15	–	Christmas Day
26	26	–	Boxing Day
27	27	–	Sunday
28	28	10	
29	30	20	
30	35	50	
31	35	70	
Jan. 1	30	60	
2	30	12	
3	28	1	Sunday
4	31	–	
5	25	–	
6	25	–	
7	30	70	
8	31	95	
9	31	100	
10	3	–	Sunday
11	31	–	
12	28	80	
13	24	–	
14	28	70	
15	9	–	
16	31	90	
17	20	–	Sunday
18	31	4	
19	30	80	

The steadiness with which the steamers fish is a valuable asset to the fishery as a whole since it tends to secure that desirable evenness in daily supply of fish for the market. Withdraw the steamers from Plymouth and supplies would fluctuate very seriously from day to day, with the result that the market would cease to attract the important class of buyer who is mainly interested in large and regular supplies of fish. This in its turn might easily lead to the more frequent occurrence of a glutted market in which price falls to a very low level because of a weakening demand. If for no other reason than this steady fishing, the steamers are a highly important section of fishing power, and a permanent reduction in their numbers would be a disquieting factor.

Size of Catches.

The amount of fish landed in any one season depends not only upon the amount of fishing power expended, but also upon the yield of the fishing. It is characteristic of the fishery that results are outstandingly good in some seasons and correspondingly bad in others ; that heavy catches are made on one day and light ones on another ; that on one and the same day, some boats land many fish, whereas others return to port empty.

Seasonal results.

The average weight per landing by steamers and motors in each of the seasons from 1924–25 to 1932–33 is shown in Table IV.

TABLE IV.

Season. (Dec. and Jan.).	Average Weight per Landing (Cwt.). Steamers.	Motors.
1924–25	40·0	20·5
1925–26	23·1	25·9
1926–27	16·6	15·9
1927–28	46·3	24·6
1928–29	27·5	23·5
1929–30	39·1	42·5
1930–31	32·7	23·3
1931–32	17·6	9·2
1932–33	34·2	20·2
	Average 30·8	Average 22·8

Looking down the results of the steam fishing it is seen that in the seasons 1924–25, 1927–28 and 1929–30, the average weight per landing was well above the mean value for the period, whereas in 1926–27 and 1931–32 it fell much below the mean. The same applies to motor landings with the single exception that the yield in 1924–25 was not outstanding. Full consideration of the probable reasons why fishing should have been very good in the three seasons mentioned, but bad in the other two, must be deferred until the biological investigations have been described. It may be said, however, that this is just what might be expected from a knowledge of the fishable stocks which frequented the grounds in those seasons.

The Drift-net as a Snare.

Variation in the size of catches arises in consequence of the nature of the fishing implement. Skippers, men of experience in the art of drifting, making full use of their knowledge and beliefs, may manœuvre their vessels to the berth they consider the best available at the moment for catching fish, but all their skill cannot ensure a good catch every time the nets are shot. This is because the instrument of capture, the drift-net, is a snare in which fish are caught only as they themselves enter it. Practical experience in drifting and a knowledge of local conditions are indispensable aids in deciding where it is best to set the snare, but the size of the catch depends upon the behaviour of the fish in the immediate neighbourhood of the set nets.

In an interesting paper, Graham (22) deals with the phenomenon of the "swim," which he defines thus: "Something happens limited in time, and space, the result of which is that herring are caught in the nets, in numbers from say five thousand to a quarter of a million per fleet of nets;

this phenomenon is called a 'swim' of herring." His provisional explanation of the swim is "that herring, in a normal state, can see the nets and avoid them, so that the sea may be full of herring, yet none caught. When, however, they are under the influence of crowd excitement (due to panic, sexual excitement or migratory impulse) herring are more or less unable to see the net, and are caught." Whether Graham's explanation holds good at Plymouth, it is impossible at present to say, but there is no doubt whatever about the fact that catches are very unequal among the vessels working in close proximity on the same night, or that catches are frequently heavier on some nights than on others.

The Effect of Gales.

A connection between stormy weather and herring catches has evidently been long recognised by Cornish fishers. Thus, Dunn (**3**) writes concerning herrings which annually visit Mevagissey Bay for spawning :—

> "One fact is certain, that they exist closely hidden near the shore ; and here they would live in undisturbed possession of their haunts but for the storms of winter, especially those blowing directly on the coast. When these happen the fish immediately leave their hidden recesses and move out into the open bay. It is only then our fishermen at Mevagissey are able to catch them ; hence our fishers are always waiting for a storm, their nets being moored with anchors at each end in the bay throughout the winter. If only an ordinary gale comes, the inside nets will get most of the fish caught ; after a violent storm the herrings will be caught in all the nets ; if there is only a strong breeze the fish will not move from their haunts. If a severe tempest is approaching the coast, the herrings by some intuitive knowledge will move out before it comes."

In an endeavour to test this belief, the strength of the wind as recorded by the Plymouth (Mount Batten) Station of the Royal Air Force and published in the Daily Weather Report of the Meteorological Office, London, has been studied in association with data on daily landings of herrings. The general procedure has been to note the wind at 1300 G.M.T., when boats are normally proceeding to sea, and at 1800 G.M.T., when the fleet is taking up position at sea on the fishing grounds. These records have then been entered in a table, opposite the catch made during the night and landed on the following morning. Working in this way through the data for the past few seasons, distinct correlation between wind and fishing results has been observed.

Reference has already been made to the fact that strong gales prevent the motor fleet from leaving harbour, but it has now to be noted that when the motors are able to resume fishing once more, catches for a few days are much above the average. Bearing in mind the suggestions made by Graham, it is as if a gale from a southerly quarter sets the fish on the move, so that many are caught. As a first example, the results for December, 1928, will be considered. There were two periods when the motor boats were prevented from fishing because of strong winds, viz. December 10th 11th, and December 22nd 26th. Table V gives data regarding the strength and direction of the wind,* and the fishing results for a few days before and after these enforced stoppages :—

TABLE V.

Wind Records and Fishing Results during December, 1928.

	Wind.				Fishing Results by Motor Boats.			
Day of Month.	1300 G.M.T.		1800 G.M.T.		Day of Month.	No. of Landings.	Average weight per Landing (cwt.).	
4	W	1	NW	1	5	60	17·5	Average weight prior to stoppage=17 cwt.
5	N	3	NNW	2	6	50	14	
6	SW	6	NW	3	7	30	6	
7	NW	3	ENE	2	8	30	19	
8	NNE	4	N	1	9	7	28	
9	–	0	SW	4	10	no fishing	–	
10	**S**	**7**	**SSE**	**6**	11		–	
11	E	2	SE	2	12	70	14·5	Average weight after stoppage =60 cwt.
12	NE	3	NE	3	13	70	59	
13	ENE	3	E	4	14	80	73	
14	SE	5	NE	4	15	30	96	
15	ENE	3	S	4	16	30	59	
18	ENE	3	SSW	4	19	40	19	Average weight prior to stoppage=19 cwt.
19	SW	3	W	3	20	30	17	
20	NNW	4	NNW	4	21	10	26	
21	–	0	E	2	22	4	15	
22	W	3	W	4	23	no fishing	–	
23	WNW	2	ESE	2	24		–	
24	**SW**	**6**	**SW**	**7**	25		–	
25	**SW**	**4**	**SW**	**6**	26		–	
26	W	4	NNW	4	27		–	
27	ESE	3	SE	4	28	10	52	Average weight after stoppage =54 cwt.
28	W	4	WSW	4	29	12	55	
29	W	5	WSW	6	30	14	43	
30	WNW	4	NNW	4	31	16	66	

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* For the convenience of readers, the following official description of the Beaufort Scale Numbers is given :—

Beaufort Scale No.	Statute Miles per hour.	Beaufort Scale No.	Statute Miles per hour.
0	Less than 1	7	32–38
1	1– 3	8	39–46
2	4– 7	9	47–54
3	8–12	10	55–63
4	13–18	11	64–75
5	19–24	12	Above 75
6	25–31		

It will be observed from Table V that the average weight per landing for the motor boats is very much greater on the days following a temporary stoppage of fishing than on those prior to the cessation. Moreover, during the stoppages themselves, the wind has blown for some time at strengths of Beaufort Scale Numbers 6 and 7 from a southerly quarter.

Similarly for the season 1929–30. During practically the whole of the first fortnight of December, 1929, the weather was wild and tempestuous, and only 3 landings were made in the 9 days from December 4th to December 12th, the market being blank for 7 days on end. On December 16th, however, 50 landings were made by motor boats with the remarkable average landing of 161 cwt. Next day there were 70 motor landings averaging 171 cwt. Thereafter, the weather remaining favourable, many motor boats were able to fish each night, but the average fell off each day, first to 83 cwt., then to 80 cwt., and was only 14 cwt. on December 20th, and 27 cwt. on December 21st. Only a few steamers had arrived at Plymouth in time for this heavy fishing, but those few obtained results similar to those of the motors. Thus, on December 16th, one steamer made a landing of 385 cwt. ; on the 17th, 4 steamers averaged 350 cwt., per landing ; on the 18th, 6 averaged 334 cwt., and on the 19th, a total of 17 averaged 288 cwt. But on December 20th, when 12 steamers landed, the average per landing fell to 50 cwt., and it stood at the still lower value of 24 cwt. on December 21st. During January, 1930, the steamers made extra heavy landings on the three days, January 12th, 13th and 14th, the averages being 70, 75 and 67 cwt. respectively. Winds from SSW and SW of Beaufort Scale Numbers 6 to 8 were blowing on January 9th and 10th, moderating on the 11th. Thus, with fishing resumed after the gale, catches were of a high order.

The season 1932–33 is of particular interest in this apparent connection between strength of wind and fishing yield. The following is an analysis of the season's catch :—

Period.	Number of Days.	Total Weight Landed. cwt.	Average Per Day. cwt.	Average per Landing.	
				Steamer. cwt.	Motor. cwt.
Dec. 1st to Dec. 6th	6	165	27	3	2
Dec. 7th to Dec. 11th	5	2,540	508	**45**	**23**
Dec. 12th to Dec. 18th	7	**36,525**	**5,246**	**67**	**32**
Dec. 19th to Dec. 26th	8	6,941	868	19	10
Dec. 27th to Jan. 3rd	8	6,760	845	21	10
Jan. 4th to Jan. 6th	3	**13,305**	**4,435**	**37**	**33**
Jan. 7th to Jan. 14th	8	11,750	1,469	22	14
Jan. 15th to Jan. 25th	11	1,546	141	14	11
Whole season	56	79,532	1,420	34·2	20·2

It is apparent from the above figures that daily results were very uneven. The two periods, December 12th to 18th and January 4th to 6th, were by far the most productive as regards total weight of fish landed.

Nearly one-half of the season's catch was landed in the seven days of the first of these periods, and another one-sixth in the three days of the second. The weight per landing for both steamers and motors was also very high. Although not so profitable in total yield, the period from December 7th to 11th was characterised by a heavy average weight per landing.

During the season, there were two periods of strong gales, the first in early December, and the second in the beginning of January.* From 1300 G.M.T. on December 6th until 0700 on December 12th the wind records taken three times daily at Mount Batten did not fall below Beaufort Scale 6 except on two occasions, and Beaufort Scale 8 was recorded throughout December 11th. The direction was mainly E.N.E. In consequence, there was no fishing by motor vessels from December 6th to December 11th except by a few larger ones on the night of December 10th. For the twelve landings made, the average was 23 cwt., which, as will be seen from the analysis given above, was fairly high. A number of steamers fished throughout the gale period, their results being good. With the gale moderating during December 12th, all vessels, both motor and steam, were able to fish that night, and on the following morning no less than 10,500 cwt. of fish were landed, representing an average steamer landing of 100 cwt. for 39 vessels, and an average motor landing of 66 cwt. for 90 vessels. Thereafter for 4 nights, a full fleet was able to work with very high yield. The second gale period extended from December 31st until January 4th, this time from the southward, with wind force from Beaufort Scale 6 to 8. There were no landings by motor drifters on January 1st, 2nd and 3rd, and although a good number of steamers continued to fish, the results were not unusually heavy. But with the return of fair weather, enabling full fishing by the motors, high average landings were realised, particularly by the motors. On January 4th, 20 motors made an average landing of 35 cwt. ; and on January 5th, 44 motors averaged 56 cwt. per landing, whereas not since December 19th had the average landing been higher than 25 cwt.

The two periods of greatest yield during the 1932–33 season, therefore, immediately followed occasions when the motor fleet had been weather-bound in harbour for some days on end. This experience, together with the other illustrations previously described, seems definitely to suggest that the herrings are in some way affected by the blowing of strong winds, so that fish are caught in great numbers in drift-nets which are set as soon as this becomes practical. There is little evidence as to what actually happens. Strong winds will, of course, increase the turbidity of the water, and possibly this may result in the fish not being able to see the nets so readily. If the fish moved under these circumstances, they would thus be more likely to become enmeshed. Possibly, in addition to increasing the turbidity of the water, strong wind action may actually induce the fish to move, and so increase the chances of fish being gilled. Whatever the cause, the apparent relation between wind and density of landing is one of practical importance.

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* Readers will be materially assisted by referring to Cooper's Fig. 1 on p. 56 of this Number. (Cooper, 1.) It should be noted that Cooper adopts the "Mean Cube Beaufort Number" as an index of the capacity of the wind to cause mixing and turbulence in the sea.

Inshore Fishing in Bigbury Bay.

On some days it is noted that the motor boats are making good landings, whereas the steamers are having a poor time. The following are a few examples from the returns of 1931–32 :—

	Steamers.		Motors.	
Date. (1931–32.)	No. of Landings.	Average Weight. (cwt.)	No. of Landings.	Average Weight. (cwt.)
Dec. 19	15	1·9	90	12
Jan. 20	30	1·4	120	35
Jan. 21	20	3·5	90	16
Jan. 27	18	3·5	90	12

This occurred when the herrings were located well inshore in Bigbury Bay. These grounds can be worked with safety by the smaller motor craft, but not by the steamers without risk of damage to both boat and gear.

Ray-netting and Trawling in Bigbury Bay.

Reference may here be made to complaints by drift-net fishermen of interference caused by other methods of fishing. It is alleged that a considerable amount of damage to drift-nets is sustained by fouling with the ropes and moorings of the large-meshed tangle nets set on the bottom in Bigbury Bay for catching rays and turbot. (*vide* Steven, **31**.) At the time of writing, negotiations are proceeding between the Sea Fisheries Committees of Devon and Cornwall, and it is hoped that a satisfactory solution of the difficulty will eventually be reached.

There is also some feeling among local drifting interests that motor trawlers fishing for spawning herrings in Bigbury Bay are doing harm to the stocks. No sound case for this objection can be made out, however, and the Devon Sea Fisheries Committee have decided to take no action.

CONCLUSION.

The yield of the Plymouth winter drift-net herring fishery is subject to daily and seasonal fluctuation. Among the contributory causes of these fluctuations are (1) variation in the number and character of the boats engaged in the fishery, and (2) variations in the intensity with which the boats are able to fish. These causes, however, do not fully account for the observed fluctuations in yield, since the results of fishing, good or bad, ultimately depend upon the number and behaviour of the fish on the grounds. It follows, therefore, that it is impossible to give a complete explanation of past fluctuations in yield, or to predict what seems likely to happen in the future, until adequate knowledge of the fish stocks has been acquired.

STUDIES OF THE FISHES LANDED.

It is convenient to commence this section with a brief summary of the more general facts concerning the herrings caught at Plymouth. Catches include fishes of three classes in varying proportions: (1) "full" fish, in which the roes and milts are sufficiently developed so as to fill or almost fill the body-cavity, (2) spawners, or "maizey" fish, in which the reproductive glands are fully mature and actually in the running condition, (3) spent fish, which for the most part have quite recently spawned. Examination of the stomachs of the fishes shows that there is no feeding. These facts prove that the fishery depends upon a concentration of fish intent on spawning. The fish have not come to feed.

But while the fish agree in the purpose for which they have come, they differ in practically all other respects. In length, individuals vary from 21 cm. to 31 cm. (8 in. to 12 in.) although a sample taken at any time during the season will probably include 50 per cent or more individuals between the lengths of 25 cm. and 28 cm. With regard to weight, Orton (**28**) has shown that for 1075 individuals the total range of variation is from 72 grm. to 218 grm. ($2\frac{1}{2}$–$7\frac{1}{2}$ oz.). Age is also variable. Fishes are mostly in the 3rd to the 7th or 8th winter of life, but an occasional individual in its 2nd winter may occur, and those in their 9th, or even older, are not uncommon. In structure and body proportions, individuals differ in such features as the size of the eye, the depth of the body, and the number of bony rays in the fins. They also differ in their number of vertebræ, and it has been shown (Orton, **28** and Ford, **8**) that, exclusive of the terminal portion of the backbone known as the urostyle, the number varies from 53 to 58. Another internal difference is in the number of pyloric cæca (Ford, **6**).

The interpretation of these differences forms an essential part of the study of the fluctuations of the commercial fishery, and in the pages which follow, an account is given of the conclusions reached.

Spawning and Spawning-time.

Direct evidence that spawning takes place in the Plymouth district is provided by records of naturally-deposited herring spawn taken by

Laboratory research vessels, although such records are surprisingly few. Only once in the past ten years has spawn been taken, when on March 3rd, 1930, eggs were brought to the surface in the trawl of s.s. *Salpa*, working on the Mewstone Grounds. Nevertheless, there are many other observations to show that spawning is intensive locally. It is of interest first to note that Matthias Dunn, the gifted fisherman-naturalist of Mevagissey in Cornwall, has given a description (Dunn, **4**) of what he believed was the actual spawning of herrings in Bigbury Bay. He says : " As to the actual spawning of Herrings, we have many times seen this going on on cold nights in December and January, in Bigbury Bay, in from fifteen to twenty fathoms of water. At such times male and female Herrings will congregate together in multitudes, and form themselves into vast columns —possibly slightly pyramidal in form—reaching from the surface to near the bottom, when they will commence a violent perpendicular action. Sometimes the top will be more than one hundred yards in diameter, and, when the column is in full swing, the mass often appears like a boiling cauldron. The uninitiated could not surmise the cause of such a perpetual din and clatter from this up-and-down motion as may be heard near by. This goes on without any horizontal movement being visible. Nor will any ordinary noise disturb them, so intent are they on their work ; and the relative position of the fish and the fishing-boats near them will often remain the same for an hour or more together. This action, no doubt, presses out the milt and roe from the male and the female, which is evidently dropped in the sea ; and the congress of life happens as the ova is sinking to the lower depths, for the spermatozoa floats—or is only of the specific gravity of the water—while the eggs are heavier, and instantly sink. Often the net will come in contact with these columns of spawning fish near their base, some fifty feet under water, and there Herrings will enter the net as thick as at the surface. When such masses are spawning, the whole sea in the neighbourhood will have a milky whiteness, caused by the surplus milt of the male." Whether or not Dunn was right in believing that he had witnessed herrings in the act of spawning, it is impossible to say, but when this talented and experienced observer describes so remarkable a phenomenon, for which no equally satisfactory alternative explanation can be advanced, it is difficult to say that he is wrong.

The presence of large quantities of maizey (spawning) fish in both drift-nets and the trawl, and the numbers of newly-hatched larval herrings which are taken in tow-nets used by the research vessels, bear out the limited direct evidence of spawning grounds inshore at points along the neighbouring coast from off Gribbon Head in Cornwall to the eastward at least as far as Exmouth in Devon. Bigbury Bay has long been regarded as one of the principal areas, no doubt because it is here that spawning shoals are most usually located, but considerable spawning must take place in other parts. Dunn (**3** and **4**) refers to spawning in Mevagissey Bay, while Wallace (**36**) records a catch of no less than 4210 recently-hatched larvæ in one ½-hour haul of the young-fish-trawl by s.s. *Salpa*, working Rame Head, bearing E. 12 miles, on February 5th, 1923—a record which strongly suggests the presence of a spawning ground near at hand. Early larvæ have also been taken in quantity at points off the Devon coast. Herrings running with spawn have been taken in Plymouth Sound and the estuaries of the Lynher and Tamar, while every year in late December and January, small drifters working out of their home ports of Exmouth, Sidmouth, Beer, etc., and fishing just off the shore in the waters of the Great West Bay, secure catches consisting almost entirely of running fish. These and other records support the belief that spawning takes place over a wider area than is commonly supposed.

It is important to fix the time at which spawning occurs. Running fish have been taken as early as September 30th (Plymouth Sound, 1925 and 1926), and as late as May 14th (trawled by s.s. *Salpa*, 1930), representing an extreme range of 7½ months. Moreover, in any one season, spawners and spents may occur in the catches at any time, making it a matter of some difficulty to decide when spawning is most general over the grounds. Observations conducted during the season 1924–25 (Ford, **9**, p. 284) indicated that spawners were chiefly in evidence in the catches of late December and the whole of January. The results of later work confirm this, but also show that considerable numbers of spawning fish are in the neighbourhood in February and March, after the drifting season has come to an end, and that these can be, and are, caught in the trawl. There is reason to believe, too, that the amount of spawning which takes place in October and November is considerably less than that in subsequent months. Although no explanation can at present be offered, it may be stated that during the past three seasons (1930–31 onwards), " maizey " fish are almost entirely absent from drift-net landings, even during the months of December and January when they would be expected. Good catches of spawning fish, however, were later secured in the trawl.

It is clear, therefore, that from October onwards, a concentration of herrings, bent on spawning, occurs off the Plymouth coasts. Many of the shoals must arrive some considerable time before the individual fishes are ready to spawn, for the catches in the earlier part of the season consist almost exclusively of " full " but not ripe herrings. Probably these shoals remain in the vicinity until spawning has been accomplished, but it is not unlikely that they are later joined by shoals which are ready to spawn almost as soon as they arrive on the grounds. In any case, it is only possible to explain the " mixed " character of landings by assuming that spawning takes place shoal by shoal throughout the season, with the result that on the same day, one boat will land " full " fish and another "spents," while one and the same catch will include fulls, spawners and spents.

Variation in Weight.

In 1914–15, a comprehensive biometric investigation of a total of 1075 herrings was carried out at the Plymouth Laboratory (*vide* Orton, **28**), which included the determination of the weight of each fish to the nearest gram. The weight was that of the ungutted fish, and the individual variation thus depended not only on the size of the fish, but also on its sexual condition. Variation due to unequal weights of stomach and gut-contents may be ignored since the winter fish at Plymouth hardly ever contain food. Fraser (**16**, p. 251) worked out a formula linking weight with length, on the basis of the data given in Orton's Table III. He found that for the total of 550 records,

$$W=0{\cdot}00000337\times L^{3{\cdot}149}$$

Where W=Weight in grammes.
L=Length in millimetres.

Fraser's formula does not take into account the individual differences in sexual condition which occur among a season's catches, but may be taken to apply to "full" fishes. From an analysis of the data given in Orton's Table IV, where the weights refer particularly to spawning fish (maturity stage VI) and spents (maturity stages VII and II), it appears as if spawning females are slightly heavier than spawning males of a similar length, while, as expected, the spents of both sexes are not so heavy as the fulls. But as the standards of sexual maturity are not sufficiently precise, no useful purpose is served in making more detailed comparisons.

The Age of Fishes Landed.

During each of the eight seasons from 1924–25 to 1931–32, estimates of the age of the herrings landed were made from their scales. Two or three scales from each fish, separately picked from the anterior region of the body near the tip of the pectoral fin, were cleaned between finger and thumb in water and mounted on a numbered glass slide, using a mixture of egg-albumin and glycerine as the adhesive. In reading a scale, the number of "summer zones" and the number of "winter rings" were both recorded (see Ford, **7**, p. 243), the clear winter-edge being counted as a completed ring. Records of age were then grouped into year-classes according to the calendar year in which the first summer zone was formed on the scale. For example, fishes caught during the season of 1924–25 which showed five summer zones and four winter rings within the winter edge, were recorded as "5 zoned 5 ringed" and assigned to the 1920 year-class. Normally, fishes older than "6-zones 6-rings" were recorded as "old" fish without any attempt to fix the age with precision.

In actual practice it was found that catches taken during the two most important months of December and January of any one season agreed sufficiently closely to warrant the calculation of a seasonal average age-composition, giving in the form of percentages the relative numbers of fishes of different ages likely to be taken in a catch at any time during that season. In the following Table VI the average percentages, according to age, are given for the eight seasons :—

TABLE VI.

Season. (Dec.–Jan.)	Percentage Numbers of Fish at the following Age.				
	3	4	5	6	Older than 6
1924–25	7·0	12·3	56·0	15·3	9·4
1925–26	5·3	15·2	14·1	47·5	17·9
1926–27	4·7	27·9	22·9	10·7	33·7
1927–28	18·6	20·4	30·9	12·0	17·1
1928–29	3·3	30·8	19·5	26·6	19·3
1929–30	1·9	18·1	35·9	15·4	28·8
1930–31	4·4	10·2	23·8	33·2	28·3
1931–32	3·4	12·6	15·0	21·3	47·7
Means	6·1	18·4	27·3	22·7	25·3 (Total=99·8%)

It is evident from the figures that the composition by age varies considerably from one season to the next. An important feature of this age-variation, however, is more clearly seen when the age data are rearranged according to the year-classes which they represent. This has been done in Table VII :—

TABLE VII.

Age of Year-class (Zones and Rings).	Percentage Numbers contributed by each of eleven Year-classes during months of December and January.										
	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	Means
3	–	–	–	7·0	5·3	4·7	18·6	3·3	1·9	4·4	3·4	6·1
4	–	–	12·3	15·2	27·9	20·4	30·8	18·1	10·2	12·6	–	18·4
5	–	56·0	14·1	22·9	31·9	19·5	35·9	23·8	15·0	–	–	27·3
6	15·3	47·5	10·7	12·0	26·6	15·4	33·2	21·3	–	–	–	22·7

Looking down the columns of Table VII it is seen that year-classes agree almost without exception in the order of the rise and fall of the percentage from the third to the sixth year. The percentage is comparatively low in the third year, rises to a maximum in the fifth, and commences to fall in the sixth. There is but one departure from this, in that year-class 1924 gave a greater percentage in its fourth year than in its fifth.

This agreement among year-classes was noted in an earlier report (Ford, **11**, p. 14) when only the results for the four seasons 1924–25 to 1927–28 were available for study. That it should hold good over the longer period of eight seasons suggests that we have to deal with something more than a fortuitous coincidence of figures, the observed agreement strongly indicating that younger year-classes replace older ones in a regular manner as the seasons go by. In considering this process of replacement, however, it is important to remember that the data relate to *commercial catches* as distinct from the *fish-stocks* from which the catches were drawn. It is true that the characters of a catch bear real relationship to the characters of the stock fished, but the former are also dependent upon the size of mesh in the nets used. Since no important alteration from season to season in the size of mesh is known to occur, the selective action of fishing may be ignored, provided that the distinction between *catch* and *stock* is recognised. The results summarised in Tables VI and VII thus show the process of replacement of older year-classes by younger, *in the fishery*. Each year-class in turn enters the fishery in its third year, reaches its maximum proportion in the catches during its fifth year, and begins to fall out in its sixth.

Further reference to Table VII shows that there is little uniformity in the contributions made by successive year-classes at the same age. Those of 1920, 1923 and 1925 gave comparatively large percentages throughout the third to the sixth years of life, whereas those of 1921, 1927 and 1928 gave correspondingly poor ones. This outstanding importance of certain year-classes and the comparative absence of others are highly significant matters which will be dealt with more fully at a later stage (p. 370). It will suffice at present to point out that in their fifth and most important year, fishes of year-classes 1920, 1923 and 1925 formed 56·0%, 31·9% and 35·9% respectively, of the season's catch. Not only this, for each in its turn remained a most important element of the catches for two or even three seasons in succession.

Before leaving this study of age-composition, attention must be drawn to the fact that all the above considerations have had to do with percentage-composition of catches and not with absolute numbers. The data tell us how many out of every hundred fish caught are of a certain age or belong to a given year-class, but they give no idea as to the absolute numbers of such fishes landed. This fact will also be recalled later.

LENGTH IN RELATION TO AGE.

It has already been stated that the length of the herrings at Plymouth varies between the limits of about 21 cm. to 31 cm. Since length increases with age, one might have expected that fishes of the same age-group would be of approximately the same length, but it is actually found that there is a wide variation in the length of fishes of the same age-group. The result is that it is quite impossible to obtain anything approaching a reliable estimate of the length of a fish merely by noting its age, or vice-versa. For example, a 3-zoned 3-ringed fish may be any length from 21 cm. to

29 cm., while an individual measuring 25 cm. in length might prove to be any age from 3 years upwards. The following Table VIII summarises results obtained during the four seasons from 1924–25 to 1927–28, and will serve to show the range and extent of the length-variation according to age :—

TABLE VIII.

Age-group.	Season.	Year-class.	No. of fishes in each of 11 length groups (cm.).											Total No.	Average length. (cm).
			21	22	23	24	25	26	27	28	29	30	31		
3-zoned 3-ringed	1924–25	1922	–	3	19	39	68	36	15	3	1	–	–	184	25·5
	1925–26	1923	2	10	9	32	44	13	3	–	–	–	–	113	24·9
	1926–27	1924	–	–	4	11	33	27	12	–	–	–	–	87	25·9
	1927–28	1925	4	18	57	71	34	4	1	1	–	–	–	190	24·2
4-zoned 4-ringed	1924–25	1921	–	–	6	13	34	67	72	53	10	2	–	257	27·0
	1925–26	1922	–	4	11	33	59	94	87	22	–	–	–	310	26·4
	1926–27	1923	–	2	13	59	88	46	19	14	2	–	–	243	25·7
	1927–28	1924	–	2	26	49	66	32	9	3	1	1	–	189	25·3
5-zoned 5-ringed	1924–25	1920	–	–	–	11	96	304	481	251	33	4	1	1181	27·4
	1925–26	1921	–	–	–	10	35	58	79	37	12	2	–	233	27·1
	1926–27	1922	–	–	3	21	54	65	48	25	2	–	–	218	26·5
	1927–28	1923	–	–	2	25	120	105	44	5	–	–	–	301	26·1
6-zoned 6-ringed	1924–25	1919	–	–	1	2	12	59	140	65	26	–	–	305	27·6
	1925–26	1920	–	–	–	6	37	106	250	304	97	6	–	806	27·9
	1926–27	1921	–	–	–	4	10	21	34	18	9	2	–	98	27·4
	1927–28	1922	–	–	–	7	27	31	31	8	5	–	–	109	26·7

That fishes of the same age-group may differ in length to the degree indicated in Table VIII is a matter which requires further consideration. A certain amount of this difference in length may be due to the fact that fishes of the same *age-group* are not necessarily all of the same absolute *age*. And this is because the method of estimating age from the number of rings and zones on the fish's scale is not able to distinguish between fishes born at different times during the same spawning season. With an extended spawning season like that at Plymouth, fishes of the same year-class may thus differ in absolute age by as much as five to six months.

Length, however, is not solely a function of age, although it is known that a herring adds something to its length during every year of its life. There is little reason for believing that two fishes, born on the same day, will reach exactly the same length after a given interval of time.

The interpretation of observed differences in length therefore necessitates enquiries in a number of different directions, the more important of which will now be dealt with.

Length (l_1) *at formation of First Winter Ring.*

It is characteristic of the Plymouth fish that the length l_1 at which the first winter ring is formed on the scale varies within wide limits. (Ford, **9**, p. 294.) Thus, for a total of 1122 fishes of year-class 1920 examined in the winter of 1924–25, l_1 varied from 6·5 cm. to 18·5 cm. Similarly, a total of 244 fishes of year-class 1921, also examined in the winter of 1924–25, varied from 8·5 cm. to 17·5 cm. In both instances, the individual values were widely dispersed over the total range of variation, so that the averages were subject to a large probable error.

Length (l_2) at formation of Second Winter Ring.

The length l_2 is also very variable. Thus, for the 244 fishes of year-class 1921 in which l_1 varied from 8·5 cm. to 17·5 cm., the value of l_2 varied from 16·5 cm. to 25·5 cm., and the average l_2 was also subject to a large probable error.

Correlation between the Values of l_1 and l_2.

In an individual fish, the difference between l_1 and l_2 is the total amount added to the length during the year which intervenes between the formation of the first and second winter rings on the scale. But, as has already been shown, the absolute age of the fish at the time when this increment was added cannot be stated with complete precision. Hence, a comparison between the observed values l_1 and l_2 for a number of fishes is in reality a comparison of the growth of fishes which probably differ in absolute age. Error from this source can be reduced to the minimum by first subdividing the fishes into groups according to the value of l_1 and then noting the value of l_2 for each of the groups. For the 4-zoned 4-ringed fishes of year-class 1921 referred to above, the following are the results :—

Values of l_1 . . .	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5
Average Values of l_2 .	17·93	18·87	19·58	20·15	20·82	21·22	22·29	22·69
$(l_2 - l_1) = t_2$ . . .	8·43	8·37	8·08	7·65	7·32	6·72	6·79	6·19

It is seen that the size of the growth increment (t_2) depends upon the length l_1, so that the larger the value of l_1, the smaller the increment. Statistical treatment of the data shows that the correlation between l_1 and the increment t_2 is significant. Hence it is possible to determine a regression equation of the form $l_2 = ml_1 + c$ which will give values of l_2 closely approximating to the observed data. Similar regression equations may be determined linking l_3 with l_2, l_4 with l_3 . . . etc. (Ford, **7**, p. 249.)

"Compensatory Growth."

This correlation between the length of a herring at the formation of a given winter-ring and the increment of length which will be added before the next ring is laid down, has been noted by other workers. For example, Watkin (**37**) writes : "It is a feature of the growth of the herring that each succeeding year's growth is less than that of the preceding year. . . . It also seems to be a general feature that the herring should approach a certain length at the completion of each of the various years' growth. If for some cause or other the fish was unable to complete this amount of growth in a particular year then it will in some measure make up the deficiency the following year, so that what may be called the phenomenon of *compensatory growth* is characteristic of the herring."

More recently, however, Hodgson (**26**) has studied the matter in an interesting way, to arrive at the conclusion that this so-called "compensatory growth" is simply explained as the natural result of comparing the growth of fishes which are at different ages. For convenience, his Fig. 30 is here reproduced as Fig. 2 below. He draws a curve AB, which he terms "the curve of ability to grow," passing through a value 8·5 cm. on the axis XY. This curve intersects the ordinate OP at point G.

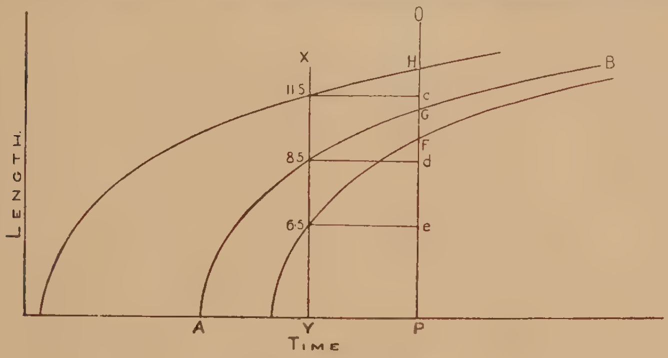

FIG. 2.—Reproduction of Fig. 30 in Hodgson (**26**). For explanation see present Text, above.

The growth made in the interval of time YP is thus given by the length Gd on the ordinate OP. Hodgson now moves curve AB to the left, keeping point A on the time-axis, until the curve cuts the XY axis at a value of 11·5 cm. instead of 8·5 cm. Under these circumstances, the growth made in the time-interval YP is given by the length Hc on the ordinate OP instead of Gd. Alternatively, the curve AB is moved to the right, still keeping point A on the time-axis, until it cuts XY at 6·5 cm. In this case the growth in the time-interval YP is given by Fe on the ordinate OP. With these things done, it is seen that Fe>Gd>Hc. That is to say, the growth made during the time YP is dependent upon the value on the XY axis through which the curve passes, the largest growth being given by the smallest value, 6·5 cm., and the smallest growth by the largest value, 11·5 cm. The sole explanation of this is that the curve AB has been started at a different point in time on the time-axis. There is no question of a difference in growth-rate, or any kind of compensatory growth, for the form of the curve has been unchanged.

The first point to be raised in connection with Hodgson's study is his "curve of ability to grow." The growth of the herring from year to year is not continuous and uniform. Seasons of growth alternate with seasons of no growth. The measurements of scales provide information as to the amounts added from year to year, but they tell us nothing concerning the time and rate at which individual increments are laid down. These facts are, of course, well known to Hodgson, and it may be assumed that he intends his curve merely as a geometric curve to show how the length increases from year to year, rather than as a growth-curve in the stricter sense.

A second point is that Hodgson gives no indication of the particular "form" of his curve AB. Admittedly, this does not affect the validity of the fact that $FE > GD > HC$, but it is important to note that the *amount* by which $FE > GD > HC$ is dependent upon the "form" of the curve as well as upon its position with relation to the time-axis.

Consider the regression equations which show the relation between l_1 and l_2, l_2 and l_3, l_3 and l_4 . . . . l_n and l_{n+1}. They are all of the general form : $Y = MX + C$

where X=Length of a herring at formation of n^{th} winter ring.
Y= ,, ,, ,, ,, $n+1^{th}$,, ,,
M=A constant of positive value less than 1.
C=A constant of positive value greater than 1.

Treating the equation $Y = MX + C$ purely as a mathematical expression, let us now apply it continuously so that having determined the value of Y for an initial value of X, we use this as a new value of X for a further calculation of Y, and so on, indefinitely. These are the results :—

Number of times the equation is operated.	Values of X.	Values of Y. ($Y = MX + C$).
1	$X_1 = 0$	$Y_1 = C$
2	$X_2 = C$	$Y_2 = C(1+M)$
3	$X_3 = C(1+M)$	$Y_3 = C(1+M+M^2)$
4	$X_4 = C(1+M+M^2)$	$Y_4 = C(1+M+M^2+M^3)$
5	$X_5 = C(1+M+M^2+M^3)$	$Y_5 = C(1+M+M^2+M^3+M^4)$
. . . .	. . . .	. . . .
n	$X_n = C(1+M+M^2+M^3+\,..M^{n-2})$	$Y_n = C(1+M+M^2+M^3+M^4+\,..M^{n-1})$

Thus at the nth operation of the equation,

$$Y_n = C(1+M+M^2+M^3+M^4\ldots M^{n-1}) = \frac{C(1-M^n)}{1-M}$$

In Fig. 3 the successive values Y_1, Y_2, Y_3 . . . Y_6 when the initial value X_1 is 0, are shown graphically, with a smooth curve passing through them.

It is seen that at the first operation of the equation, as represented by one unit along the time-base, the value of Y is C. After the second operation, Y has increased by an additional amount MC, which is less than C

because M is less than unity. The third operation adds a further amount M^2C, which is again a proportionate part of the previous increase. After the sixth operation, the total increments which have been added are C, MC, M^2C, M^3C, M^4C and M^5C, each of these being equal to M times the previous increment. Clearly, therefore, the continuous operation of the equation is bringing the value of Y nearer and nearer to a limiting value by permitting an increase in Y which is always M times the previous increase. It is simple to ascertain what the limiting value actually is, by observing that $Y_n = \frac{C(1-M^n)}{1-M}$. As n is increased, M^n decreases, so that ultimately M_n becomes zero, and hence the limiting value $Y_\infty = \frac{C}{1-M}$.

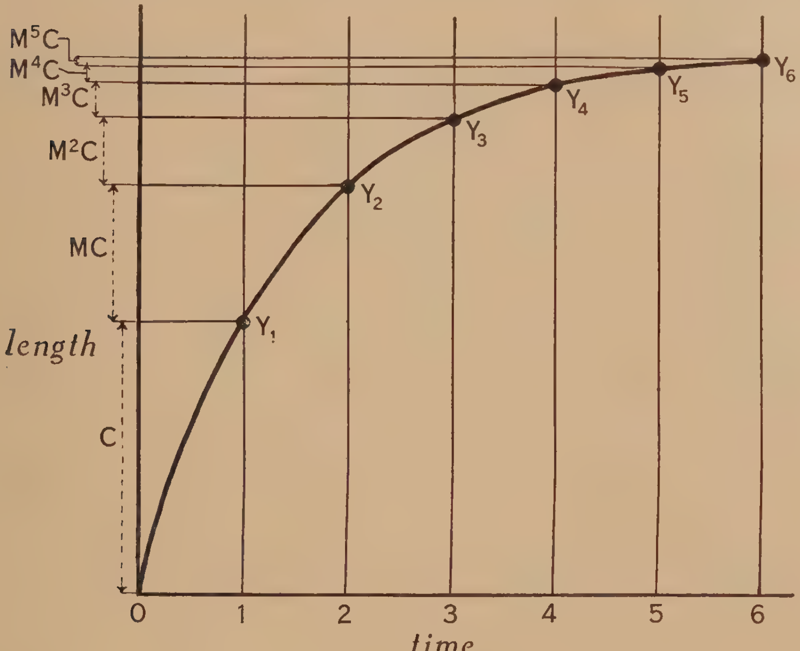

FIG. 3.—For explanation, see Text, p. 330.

In Fig. 4, on p. 332, the curve given in Fig. 3 has been re-drawn in triplicate from three points along the time-base. It is seen that on the ordinate at time 5, $BA > CB > DC$. This is clearly a repetition of Hodgson's result and, like his, is entirely due to the fact that the three curves occupy different positions in relation to the time-axis. But in Fig. 4, the actual "form" of the curve is known, whereas in Hodgson's figure it is not.

Attention is now directed to Fig. 5, which resembles Hodgson's figure in that three curves commence from different points along a time-base and intersect the ordinates XY and OP. Here again, $Fe > Gd > Hc$, but for a different reason. Whereas in Hodgson's figure and also in Fig. 4, a single curve is drawn in three alternative positions, in Fig. 5 *the three curves are all different*. Curve 1 is that resulting from the continuous operation of the equation $Y = \cdot 5X + 15$; curve 2, from the equation $Y = \cdot 6X + 12$; and curve 3 from the equation $Y = \cdot 7X + 9$. All three curves are gradually approaching the limiting value of $\frac{C}{1 - M}$, which in each case is 30. In consequence of the order in which the curves are placed with regard to time, they can be extended indefinitely to the right without ever meeting. Wherever the ordinate OP is erected, Fe will always be greater than Gd, and Gd greater than Hc. But the *amount* by which these increments will differ will depend not only upon the length of time the curves have been extended from their commencement, but also upon their "forms."

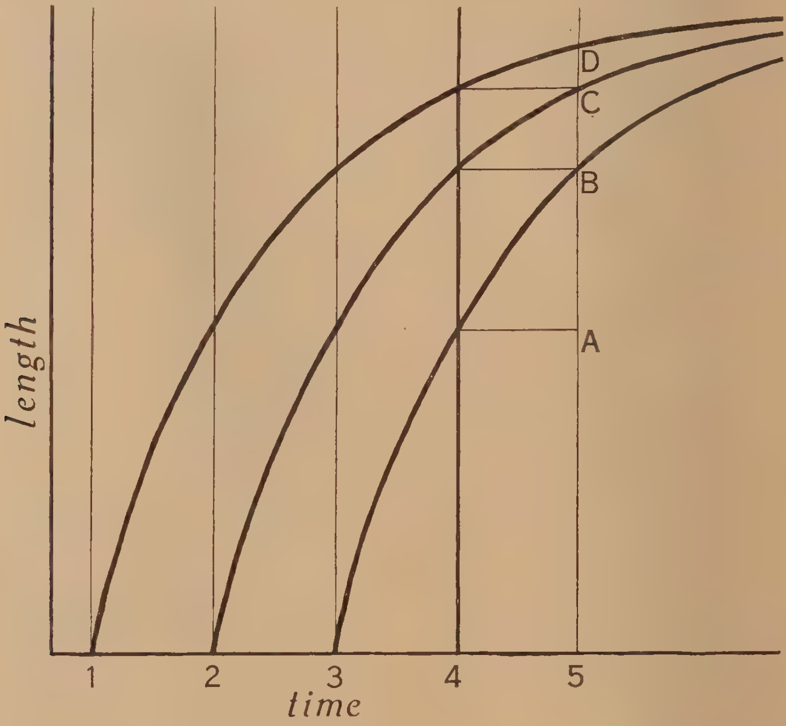

FIG. 4.

These theoretical considerations show that Hodgson's explanation of "compensatory growth" in the herring is subject to reservation. He says: "If we call the curve AB, the curve of ability to grow, we see that with increase of age there is less ability to increase length and consequently the larger and older fish of any given growth period will grow less than the smaller and younger fish." But it is necessary to add that the "curve of ability to grow" may itself be subject to variation from fish to fish, with important consequences.

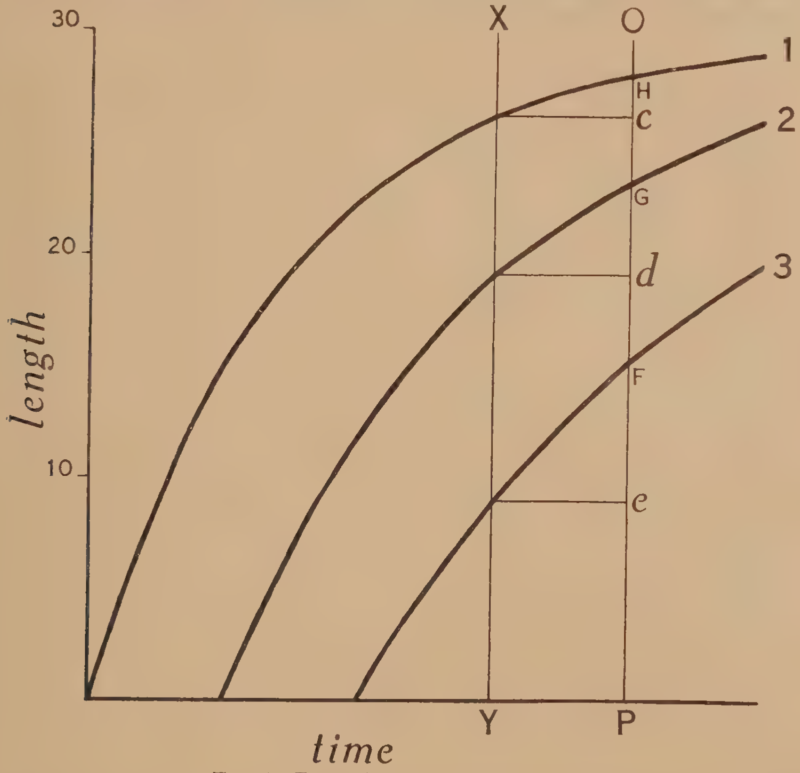

Fig. 5.—For explanation, see Text, p. 332.

Growth in Length in different Geographical Areas.

In earlier papers an endeavour was made to show that regression equations can be used as a technique for the comparison of growth in length in different geographical areas. The method has since been developed with rather instructive results. In illustration, data given by Gilson (**21**, p. 50, in Table XIII) regarding the mean lengths from l_1 to l_9 for spent herrings taken from the region Griz-Nez to Ostende will now be used. Take the equation $Y = {\cdot}56X + 11{\cdot}5$ and substitute Gilson's l_1 of 9·96 cm. for X. The value of Y (representing l_2) is given by $\cdot 56\,(9{\cdot}96) + 11{\cdot}5 = 17{\cdot}08$ cm. as against the observed value of 17·19 cm. Next, using the value 17·08 as a new value of X, a new value of Y (this time representing l_3) is given by $\cdot 56\,(17{\cdot}08) + 11{\cdot}5 = 21{\cdot}06$ cm., as compared with the actual l_3 of 21·05 cm. Similarly, the substitution of 21·06 for X will provide a value of Y which represents l_4. Working in this way, a complete alternative set of calculated values for $l_2, l_3 \ldots l_9$ can be obtained and compared with Gilson's data :—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
Gilson's means	9·96	17·19	21·05	23·14	24·29	25·20	25·58	26·00	26·50
By equation	9·96	17·08	21·06	23·29	24·54	25·24	25·64	25·86	25·98

It is seen that with the exception of the period from l_8 to l_9 the equation has given values which closely approximate to the observed data. That is to say the herrings represented by Gilson's data had, on average, added to their length yearly in a regular manner, whereby the increment of length added in each succeeding year was approximately ·56 times the increment added in the previous year.

The single equation $Y = {\cdot}56X + 11{\cdot}5$ is thus all that is necessary for determining how the Belgian fish add to their length from year to year. It is especially convenient as a means for comparing the Belgian results with those from other places where the average l_1 may be higher or lower than 9·96 cm. For instance, Gilson gives Hodgson's data for herrings of the southern North Sea ($l_1 = 8$ cm.), and also those of le Gall's *Type côtier* ($l_1 = 11{\cdot}88$ cm.) and *Type atlantique* ($l_1 = 12{\cdot}49$ cm.) from the English Channel. By determining the values of Y when X is 8, 11·88 and 12·49 respectively, using the Belgian equation, and comparing them with Hodgson's and le Gall's l_2 values, any difference in growth is at once revealed. In the following table Hodgson's and le Gall's data are fully compared with those given by continuous operation of the Belgian equation :—

Southern North Sea.		Type Côtier.		Type Atlantique.	
(Hodgson.)	Equation.	(le Gall.)	Equation.	(le Gall.)	Equation.
$l_1 = 8$	8·0	$l_1 = 11{\cdot}88$	11·88	$l_1 = 12{\cdot}49$	12·49
$l_2 = 16$	16·0	$l_2 = 18{\cdot}46$	18·15	$l_2 = 19{\cdot}19$	18·49
$l_3 = 20–21$	20·45	$l_3 = 21{\cdot}72$	21·66	$l_3 = 22{\cdot}46$	21·85
$l_4 = 23$	22·95	$l_4 = 23{\cdot}30$	23·62	$l_4 = 24{\cdot}25$	23·74
		$l_5 = 24{\cdot}50$	24·72	$l_5 = 25{\cdot}40$	24·79
		$l_6 = 25{\cdot}54$	25·34	$l_6 = 26{\cdot}17$	25·38
		$l_7 = 26{\cdot}40$	25·69	$l_7 = 26{\cdot}94$	25·72

It is seen that Hodgson's data as a whole and le Gall's data for the *Type côtier* as far as l_6 are well fitted by the Belgian equation. The only important difference between the fishes in the three cases is in the value of l_1. On the other hand, the rate of increase in length of le Gall's *Type atlantique* is distinctly faster than that given by the Belgian equation.

Good material for a second illustration is provided by a sample of Icelandic herrings of the year-class 1906, taken 3 km. N. of Siglunaes on July 25th, 1908. Data are given by Hjort (**23**, p. 119, Collection 16). The mean values of l_1 to l_{12} as recorded by Hjort, and the corresponding values calculated from the continuous operation of the equation $Y = {\cdot}742X + 9{\cdot}57$ are given below :—

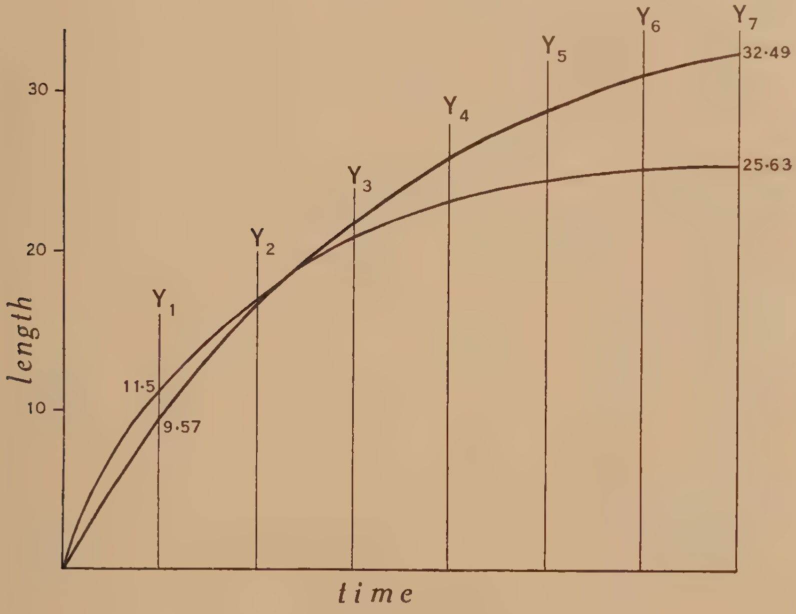

FIG. 6.—Comparison of growth in southern North Sea with that in Iceland.

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9	l_{10}	l_{11}	l_{12}
Hjort	8·7	15·7	21·4	26·0	29·0	30·8	32·2	33·2	34·2	35·0	35·8	36·3
Equation	8·7	16·0	21·5	25·5	28·6	30·8	32·4	33·6	34·5	35·2	35·7	36·1

Here again a single equation has yielded a close approximation to observed data. But this equation is not the same as the one which satisfied Gilson's, Hodgson's and le Gall's data. The difference between them may be demonstrated by continuously operating both from a commencing value $X=0$. In effect this is equivalent to starting two curves from the same point in time, as in Fig. 6. The degree to which the curves diverge is a measure of the difference in the rate which at length is added. The results are as follows :—

Equation.	Y_0	Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7
$Y = {\cdot}742X + 9{\cdot}57$.	0	9·57	16·67	21·94	25·85	28·75	30·90	32·49
$Y = {\cdot}56X + 11{\cdot}50$.	0	11·50	16·94	20·98	23·25	24·52	25·23	25·63

The Icelandic growth is clearly of a totally different order from that of the southern North Sea and English Channel, both in the successive yearly increments and the limiting value towards which the total length tends to approach each year. The Icelandic limit $\frac{C}{1-M}$ is $\frac{9{\cdot}57}{1-{\cdot}742} = 37{\cdot}1$ cm., whereas the southern North Sea limit is $\frac{11{\cdot}5}{1-{\cdot}56} = 26{\cdot}1$ cm.

The above examples indicate (1) that in many cases the successive yearly increments which a herring adds to its length decrease in magnitude in something very nearly approaching geometric progression, and (2) that there are real differences in growth between herrings of different geographical areas. The first of these points is hardly what might be expected at first sight. And yet, when it is seen how closely the Icelandic data are matched by the equation values over a period of twelve years, it is impossible to ignore the observation. The result would seem to suggest that the Icelandic fish had succeeded in growing, as it were, "according to plan," whereby each succeeding year an increment of length is to be added which shall always be about ·742 times the increment added the year before. Returning to the original data and noting the actual annual increments, it is possible to determine how much they deviate from those which would have been added if growth had been strictly according to "plan" :—

Actual Increments.	Increments given by Growth-Equation.	Difference.
$t_2 = l_2 - l_1 = 7{\cdot}0$ cm.	7·3 cm.	·3 cm.
$t_3 = l_3 - l_2 = 5{\cdot}7$	5·5	·2
$t_4 = l_4 - l_3 = 4{\cdot}6$	4·0	·6
$t_5 = l_5 - l_4 = 3{\cdot}0$	3·1	·1
$t_6 = l_6 - l_5 = 1{\cdot}8$	2·2	·4
$t_7 = l_7 - l_6 = 1{\cdot}4$	1·6	·2
$t_8 = l_8 - l_7 = 1{\cdot}0$	1·2	·2
$t_9 = l_9 - l_8 = 1{\cdot}0$	·9	·1
$t_{10} = l_{10} - l_9 = {\cdot}8$	·7	·1
$t_{11} = l_{11} - l_{10} = {\cdot}8$	·5	·3
$t_{12} = l_{12} - l_{11} = {\cdot}5$	·4	·1

The difference, sometimes positive and sometimes negative, is not very large when expressed in absolute lengths as above, and therefore gives the impression that growth follows the geometric law with consistent regularity, leaving but little evidence of any variation resulting from annual differences in conditions for growth. Some light is thrown on this matter, however, if the proportion between a given increment and the preceding one is compared with the theoretically fixed value of ·742 :—

$$\text{Ratio}: \frac{t_{n+1}}{t_n}$$

$$\frac{t_3}{t_2} = \frac{5\cdot7}{7\cdot0} = \cdot81$$
$$\frac{t_4}{t_3} = \frac{4\cdot6}{5\cdot7} = \cdot81$$
$$\frac{t_5}{t_4} = \frac{3\cdot0}{4\cdot6} = \cdot65$$
$$\frac{t_6}{t_5} = \frac{1\cdot8}{3\cdot0} = \cdot60$$
$$\frac{t_7}{t_6} = \frac{1\cdot4}{1\cdot8} = \cdot78$$
$$\frac{t_8}{t_7} = \frac{1\cdot0}{1\cdot4} = \cdot71$$
$$\frac{t_9}{t_8} = \frac{1\cdot0}{1\cdot0} = 1\cdot00$$
$$\frac{t_{10}}{t_9} = \frac{\cdot8}{1\cdot0} = \cdot80$$
$$\frac{t_{11}}{t_{10}} = \frac{\cdot8}{\cdot8} = 1\cdot00$$
$$\frac{t_{12}}{t_{11}} = \frac{\cdot5}{\cdot8} = \cdot625$$

The values of the ratio $\left(\frac{t_{n+1}}{t_n}\right)$ vary between the limits of ·6 and 1·0, thus causing the length l_n to be sometimes greater and sometimes less than the value which would be attained if the ratio had remained steady at ·742. These annual fluctuations in growth rate are not very large when expressed in absolute units in length, particularly in the later years of life. Nevertheless, they must be regarded as real differences due to annual changes in conditions for growth. The geometric law making the best fit to the observed results may be regarded as the smoothing out of real fluctuations which are likely to recur year after year. Viewed in this light there should be no occasion for surprise, either that it should be possible to formulate a law fitting growth with the passage of time, or that individual increments of growth should differ from those indicated by that law. If there is anything unexpected in the matter it is that the law arrived at should be of the particular nature indicated above, although even here it is not necessary to insist that herring-growth is strictly of the geometric type whereby annual increments become less and less in constant ratio. Very possibly the total length does not truly approach an asymptotic limit, although its value at each year for many years in succession may for all practical purposes be sufficiently closely portrayed by a mathematical law which *does* demand an asymptotic limit.

Practical Application of Technique.

Using this technique on data given by Hjort (**23**), comparisons of growth have been made between samples of herrings obtained from various places in the North Sea. The results are shown in Table IX, the appropriate equation, its period of operation and the limiting value set by it, being given in each instance :—

TABLE IX

Locality.	Reference to Sample (Hjort, **23**).	Period of operation of equation.	Equation.	Limiting value. (cm.)
Lowestoft	Collection 25, pp. 147 and 149			
	Year-class 1904	l_1 to l_5	$Y = \cdot 6X + 11\cdot 0$	27·5
	Year-class 1902	l_1 to l_7	$Y = \cdot 635X + 10\cdot 0$	27·4
Grimsby	Collection 26, p. 155			
	Year-class 1904	l_1 to l_5	$Y = \cdot 62X + 10\cdot 5$	27·6
Faroes	Collection 21, p. 136			
	Year-class 1904	l_1 to l_4	$Y = \cdot 6X + 12\cdot 6$	31·5
Shetlands	Collection 24, pp. 141–144			
	Year-class 1904	l_1 to l_5	$Y = \cdot 6X + 12\cdot 6$	31·5
	Year-class 1903	l_1 to l_6	$Y = \cdot 6X + 12\cdot 6$	31·5
	Year-class 1900	l_1 to l_8	$Y = \cdot 6X + 12\cdot 6$	31·5
	Year-class 1902	l_1 to l_7	$Y = \cdot 62X + 11\cdot 8$	33·1
Iceland	Collection 15, p. 111			
	Year-class 1895	l_1 to l_{13}	$Y = \cdot 74X + 9\cdot 5$	36·5
	Collection 16, p. 119			
	Year-class 1896	l_1 to l_{12}	$Y = \cdot 742X + 9\cdot 57$	37·1
Iceland	Collection 17, pp. 123 and 125			
	Year-class 1901	l_1 to l_8	$Y = \cdot 74X + 9\cdot 8$	37·7
	Year-class 1897	l_1 to l_{12}	$Y = \cdot 74X + 9\cdot 4$	36·2

It is seen that the limiting value rises from about 27·5 cm. off Lowestoft to 37–38 cm. in Iceland. In the equations there is a marked change in the value of M and a less pronounced change in C. This alteration in limiting value and form of equation from southward to northward brings to mind the fact that the number of vertebræ shows a similar tendency. (*Vide* Schnakenbeck **29** and **30**.)

One important matter not taken into account in the results of Table IX is the possibility that individual samples are " mixtures " which ought not to be treated as homogeneous for the study of growth in length. It is emphasized, therefore, that these results are in no sense to be regarded as a critical analysis of the growth in the different regions dealt with. They are merely intended to show the kind of regional differences in growth which are revealed by using growth equations. The samples considered are a selection from Hjort's invaluable data which lend themselves fairly easily to treatment.

" *Mixed* " *Growth.*

Many of Hjort's samples cannot be fitted with a single equation in the manner illustrated in previous pages. Nevertheless it is found that two equations instead of one will satisfy the data. Hjort's Collection 27, Year-class 1900, caught off North Shields (Hjort, **23**, p. 159), may be used as an initial illustration :—

l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
9·0	16·1	20·0	22·3	23·6	24·6	25·3	26·0	26·6

t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9
7·1	3·9	2·3	1·3	1·0	0·7	0·7	0·6

$\frac{t_2}{t_1}$	$\frac{t_3}{t_2}$	$\frac{t_4}{t_3}$	$\frac{t_5}{t_4}$	$\frac{t_6}{t_5}$	$\frac{t_7}{t_6}$	$\frac{t_8}{t_7}$	$\frac{t_9}{t_8}$
·56	·55	·59	·565	·77	·70	1·0	·86

Looking at the values of the ratio $\frac{t_{n+1}}{t_n}$, it is seen that up to l_5 it varies only between ·55 and ·59, but that there is then a marked rise to ·77. Not at any subsequent time does the ratio fall to the level at which it remained during the earlier years. Using the equation $Y = \cdot 57X + 10\cdot 9$ from a commencing value of $X = 9\cdot 0$ we get

l_1	l_2	l_3	l_4	l_5
9·0	16·0	20·0	22·3	23·6

These values are almost identical with the observed values, and represent growth which is steadily falling off towards an asymptotic limit of $\frac{10\cdot 9}{\cdot 43} = 25\cdot 3$ cm. It is obvious, however, that a change occurs at l_5. Let us therefore try a second equation, $Y = \cdot 75X + 6\cdot 95$, commencing with $X = 23\cdot 6$:—

l_5	l_6	l_7	l_8	l_9
23·6	24·6	25·4	26·0	26·5

These results are a close approximation to the observed values, and represent growth which is steadily falling off towards a limiting value of $\frac{6\cdot 95}{\cdot 25} = 27\cdot 8$ cm., as compared with the limit of 25·3 cm. towards which the curve of growth up to l_5 was approaching.

The Norwegian samples provide numerous cases of growth which cannot be fitted by a single growth equation. Hjort's data concerning fishes of year-class 1904 make an instructive study in this connection. In the following table his data of Collection 5 from Leinæs Hammerö (p. 52) and of Collection 9 from 60° 30′ N. 3° 30′ E. (p. 71) are compared. In the case of the increments t_1, t_2, etc., the year when the increase was made is shown :—

						1905.	1906.	1907.	1908.
	l_1	l_2	l_3	l_4	l_5	t_2	t_3	t_4	t_5
Collection 5	7·0	11·9	15·4	19·3	22·7	5·0	3·4	3·9	3·4
Collection 9	8·4	15·9	21·9	25·3	27·6	7·5	6·0	3·5	2·2

Consider the two equations beneath in connection with the growth from l_1 to l_3 :—

$$\text{(1)} \quad Y = \cdot695X + 7\cdot1 \qquad \text{and (2)} \quad Y = \cdot80X + 9\cdot18$$

$$\text{The limiting value for (1) is given by } \frac{7\cdot1}{\cdot305} = 23\cdot3 \text{ cm.}$$

$$\text{The limiting value for (2) is given by } \frac{9\cdot18}{\cdot20} = 45\cdot9 \text{ cm.}$$

Applying equation (1) for a commencing value of 7·0 cm. and equation (2) for a commencing value of 8·4 cm. we get

	l_1	l_2	l_3
Equation (1)	7·0	11·96	15·41
Equation (2)	8·4	15·90	21·90

Comparing these results with Hjort's data it is seen that equation (1) reproduces the values for Collection 5 and equation (2) those for Collection 9. Thus the growth of the fishes of Collection 5 during the years 1905 and 1906 was quite different from the growth of the fishes of Collection 9 during the same two years.

Next, consider two further equations in connection with the growth from l_3 to l_5 :—

$$\text{(3)} \quad Y = \cdot87X + 5\cdot9 \text{ and (4)} \quad Y = \cdot615X + 11\cdot9$$

The limiting values are :—

$$\text{for (3)}\ldots\ldots \frac{5\cdot9}{\cdot13} = 45\cdot4 \text{ cm.}$$

$$\text{for (4)}\ldots\ldots \frac{11\cdot9}{\cdot385} = 30\cdot9 \text{ cm.}$$

Applying equation (3) for a commencing value of 15·41, and equation (4) for a commencing value of 21·90, the following values are obtained :—

	l_3	l_4	l_5
Equation (3)	15·41	19·3	22·7
Equation (4)	21·90	25·37	27·5

That is to say the growth of the fishes of Collection 5 from l_3 to l_5 is reproduced by equation (3), and that of the fishes of Collection 7 by equation (4). Hence in 1907 and 1908, as well as in 1905 and 1906, the growth was different for the two collections.

Summarising, it is now seen that Collection 5 shows a growth from l_1 to l_3 towards a limit of about 23 cm., followed by a growth from l_3 to l_5 towards the much higher limit of about 45 cm. The change in growth rate results in the increment t_4 added during 1907 being greater than t_3 laid down in 1906. In contrast, Collection 9 shows a growth from l_1 to l_3 towards a high limit of approximately 46 cm., followed by a growth from l_3 to l_5 towards a much lower limit of about 32 cm. The change in growth rate at l_3, however, is not so self-evident as in Collection 5 (where the dominance of t_4 over t_3 is visible) and only becomes apparent when growth is analysed.

How are these results to be interpreted ? A reasonable answer to this question is twofold in nature :—

(*a*) That the fishes of Collection 5 were under quite different conditions for growth during 1905 and 1906 from those under which the fishes of Collection 9 were growing during the same period. Similarly during 1907 and 1908.

(*b*) That the fishes of the same Collection, whether 5 or 9, were not under the same conditions for growth during 1905 and 1906 as they were during 1907 and 1908.

Growth in Length as Evidence of Migration.

If the conclusions (*a*) and (*b*) just given are substantially correct, it seems to follow that the growth characters revealed by the study of scale-measurements can be used as clues to herring migrations. This point has been strongly advocated by Lea (**27**). The Norwegian investigator contends that the history of growth of the different year-classes occurring in a catch may exhibit certain extremely characteristic and striking peculiarities which, precisely because they deviate from the normal, may very easily be observed and recognised. He has no hesitation, therefore, in asserting that Norwegian herrings occurred in the spawning condition off the Faeroes in 1910, intermixed with non-Norwegian (Faeroese) herrings, and also suggests that spring-spawning herrings taken off the Shetlands in March-April, 1923, were also Norwegian fish, especially of the year-class 1918. He also shows how the fish caught in the Skagerak by Swedish and Norwegian vessels fishing independently agreed in growth characters not only with one another but with those from shoals met with at the west coast of Norway a little south of Cape Stadt. All belonged to shoals or groups of immature Norwegian herring. Thus Lea arrives at the conclusion that " . . . it is possible to identify or recognise Norwegian herring even if they occur in localities where one would not have expected them." The investigations of Storrow (**32**) also, in distinguishing between growth in " narrow seas " and that under " oceanic " conditions, follow very similar lines as regards their underlying principle. All that is claimed for the method of calculating growth equations in this type of investigation is that it provides a convenient and practical technique of growth-analysis which will readily reveal the characteristics of growth in different places, and facilitate the carrying out of growth-comparisons. While Lea and Storrow would be directly influenced in their judgment by the absolute size of the increments added to its length by a fish during a period of time, the investigator using the equations would review the same basic facts, but in terms of the growth-equations reproducing the increments, rather than of the increments themselves. As with any other method which seeks to trace the migrations of herrings by indirect means, however, one needs to consider when the technique can be legitimately applied and how the results of its use must be interpreted.

The Plymouth Shoals.

In this discussion on growth in length we have been drawn away from the situation at Plymouth. Growth studies of the herrings visiting Plymouth waters have shown that the shoals are "mixed" in a complex manner as regards growth in length. It is impossible to give a single equation which, by continuous operation, will give successive values l_2, l_3, etc., that may be considered as a "type" of growth representative of the Plymouth fish. There is no such "type." On the other hand, it has previously been suggested (Ford, **9**, p. 299) that if the spawning shoals visiting Plymouth are assumed to have come partly from the more enclosed waters of the English Channel and partly from the more open waters at the Atlantic end of the Channel (conditions for growth in these two areas being different), the complex growth-data can be interpreted in terms of migratory changes.

It has already been demonstrated (p. 334) that at the extreme eastern end of the Channel and the Southern Bight, growth is not greatly different from that reproduced by the equation $Y = \cdot56X + 11\cdot5$. It has also been shown (Ford, **12**) that fishes caught off the Sussex coast, as well as those which Hodgson terms his "Channel type," differ from the above only in the length l_1, growth being otherwise of a similar order. Coming westward to Portland and Plymouth, le Gall (**18**, p. 47) gives data concerning samples taken from catches off Brixham in Portland Bay, and in the bay of Plymouth :—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7
Brixham . .	12·20	18·30	21·00				
Plymouth . .	11·88	18·46	21·72	23·30	24·50	25·54	26·40

The Brixham sample is satisfactorily fitted by the equation $Y = \cdot56X + 11\cdot5$ and the Plymouth data, which Gilson refers to as le Gall's "type côtier," have already been shown (p. 334) to be in accordance with this same equation. That is to say, samples at Brixham and Plymouth, examined by le Gall, have been found which show growth of the same character as that of fishes from the Southern Bight and eastern English Channel. But le Gall in the same paper also gives data from the coast of Brittany :—

	l_1	l_2	l_3	l_4	l_5	l_6
Audierne	10·98	17·40	21·20	22·98	24·40	25·17
Penmarc'h	11·50	17·50	20·30	22·00		
Le Croisic	12·17	18·60	22·00	23·70	25·00	25·50

Of these it can be said that the samples from Audierne and le Croisic are reasonably well fitted by the equation used above, and even those from

Penmarc'h are not greatly different. From the Southern Bight to Brittany, therefore, herrings have been taken which have all grown according to one and the same growth curve, although differing in the length l_1.

But while this is true, it must be observed that not all the herrings in the Plymouth area have growth-characters which are fitted by the equation $Y = \cdot56X + 11\cdot5$. Thus, it was shown above on p. 334 that herrings caught in the Bay of Plymouth by le Gall and called by him the "type atlantique" do not conform to the equation. Nor will all the data collected at the Plymouth laboratory be thus satisfied. On the contrary, it becomes necessary to utilise fresh equations which give a higher limiting value than that imposed by the equation $Y = \cdot56X + 11\cdot5$. In this connection, it is of interest to refer to data brought together by Watkin (**48**) and referring to herrings taken in south-western waters. In his Table XX, on p. 87, Watkin records the average size at the formation of each winter ring for (*a*) drift herrings caught mainly in statistical region VIIg off the south-west coasts of Great Britain, (*b*) trawled herrings of the "Smalls," and (*c*) drift herrings taken at Plymouth and examined by Ford (**9**, p. 295) :—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
(*a*)	12·6	20·2	24·0	26·2	27·4	28·2	28·8	29·5	29·9
(*b*)	15·9	23·6	25·4	27·2	28·0	28·7	29·6	29·8	30·0
(*c*)	13·88	21·03	24·64	27·02					

Considering (*a*) above, it has been found that the lengths l_1 to l_5 are in accord with the results of the repeated operation of equation $Y = \cdot53X + 13\cdot5$, and the lengths l_5 to l_9 to a second equation $Y = \cdot85X + 4\cdot87$. That is to say, the drift fish in region VIIg grow from l_1 to l_5 towards an asymptotic limit of $\frac{13\cdot5}{1-\cdot53} = 28\cdot7$ cm., and from l_5 to l_9 towards a higher asymptotic limit of $\frac{4\cdot87}{1-\cdot85} = 32\cdot5$ cm. The observed values of l_5 to l_9 and the values calculated from the two equations are given together below, and it will be seen that they are in close agreement :—

	l_1	l_2	l_3	l_4	l_5	l_6	ll_7	l_8	l_9
Observed . .	12·6	20·2	24·0	26·2	27·4	28·2	28·8	29·5	29·9
Equation . .	12·6	20·18	24·20	26·32	27·45	28·20	28·84	29·39	29·86

Turning next to the fish from the "Smalls," (*b*) above, it is found that except for the one period l_1 to l_2, the growth corresponds with that of the drift fish from VIIg, in that from l_2 to l_5 the equation $Y = \cdot53X + 13\cdot5$ applies, and from l_5 to l_9, the equation $Y = \cdot85X + 4\cdot87$:—

	l_1	l_2	l_3	l_4	l_5	l_6	l_7	l_8	l_9
Observed . .	15·9	23·6	25·4	27·2	28·0	28·7	29·6	29·8	30·0
Equation . .	19·06	23·6	26·0	27·28	27·96	28·64	29·22	29·71	30·12

The "Smalls" fish thus differ from the drift fish from VIIg in that they are on an average larger at l_1 and grow to a greater size at l_2; subsequently, however, their growth is of a similar order.

The Plymouth data, (*c*) above, like those of the drift fish from VIIg are satisfied by the equation $Y = \cdot 53X + 13\cdot 5$ from l_1 to l_3:—

	l_1	l_2	l_3	l_4
Observed . . .	13·88	21·03	24·6	27·02
Equation . . .	13·88	20·86	24·56	26·52

All the foregoing observations have a bearing upon the composition of the herring shoals which come to Plymouth in the winter and spring for spawning. Some of the fish are indistinguishable in growth from fishes taken in the Atlantic fisheries; others resemble fishes taken in the eastern part of the English Channel, while others, again, show a "mixed" growth in the sense that they resemble Atlantic fish at some part of their growth, and the more easterly fish at another. A reasonable interpretation of these variations in growth character is that the Plymouth spawning grounds are visited by shoals coming both from the westward and the eastward. Those fishes coming from the westward will have fed and grown under Atlantic conditions during the summer preceding spawning, and will have grown more than those of a corresponding size and age which have remained within the more enclosed waters of the Channel. Furthermore, it is necessary to believe that fishes which come from the east or west to spawn do not necessarily return always to the same feeding grounds from which they come. In other words, the study of the growth in length from year to year is an indirect means of determining the nature and extent of the migrations between the Plymouth spawning area and the feeding grounds of the Channel and Atlantic. Concerning these migrations, Matthias Dunn (**4**) has written :—

"On our coast (Devon and Cornwall), after spawning, Herrings generally take off into deep water, and seldom remain in one locality unless food is plentiful; and, as the summer advances, they generally find themselves far out in the deep waters of the Channel or in the Atlantic. When the autumn arrives . . . they gather themselves in large schools and move landwards to the necessary weedy coral or stony bed wherein to deposit their eggs. . . . One of the largest migrations ever noted on our southern coasts was in the autumn of 1892. Late in October our fishing boats fell in with quantities of Herrings some fifteen miles south of the Eddystone, while fishing for mackerel there, and, although only mackerel nets were at first used, so plentiful were they, that it was nothing uncommon for boats nightly to catch ten thousand herrings in them. Nothing seemed to disturb them, and, although apparently wandering at leisure, eventually it was found that they gradually but surely kept up a northerly course, and early in December finally reached their spawning grounds on the Devon coast—to the east of Plymouth. . . . This is a sample of how Herrings generally migrate around the coasts; and, probably, the events connected with the migrations of the Herrings in the North Channel (i.e. off north coast of Cornwall) in their various stages, move much on the same lines. For some years past these northern fish have been in greater numbers than the southern schools, and in their spawning migration seem to strike the land somewhere to the north and east of Port Isaac. When their intuitions tell them that the range of ground for spawning purposes is unfit or insufficient for their wants in that immediate neighbourhood, they gradually drop down the coasts, leaving ample numbers to cover grounds near Padstow, Newquay, St. Ives, and Mounts Bay. Moreover, I think there can be no doubt that sometimes they have been in such numbers as to necessitate their moving further along the coast into the English Channel, and to have joined their friends near Plymouth in Bigbury Bay. For many years, off and on, when pilchards are migrating late in November, quantities of herrings will sometimes pass with them; and at other times Herrings will migrate along distinct from the pilchards. We have many times traced these fish from the Lizard to beyond Plymouth."

This scheme of migration, visualised by Dunn, appears to express, as clearly as possible, the general conception arrived at by the comparison of growth-rates among the fishes concerned, and there seems no necessity to suggest any radical alteration in the events described. The only addition considered necessary is that shoals do not always return to the grounds from which they came, with the result that "mixed" growth is a characteristic of the fishes over the whole area of distribution covered by the migratory cycles.

GENOTYPES IN THE HERRING.

In foregoing pages, differences in rate of growth in length from one geographical region to another were discussed. Throughout the discussion, however, it was assumed that a "herring" was a "herring," the distinction between *phenotype* and *genotype* being ignored. The degree to which the observed variation in growth in length among the Plymouth fishes is genotypic as opposed to phenotypic, that is to say, the degree to which it is due to qualities inherited from the ancestors of the fish as opposed to qualities due directly to the conditions under which the fish has grown up, is a question for future investigation, but much work has already been done in an endeavour to recognise genotypes at Plymouth by analysing counts of the number of vertebræ. Many samples, taken at random from commercial catches, have been examined, and appreciable differences in number of vertebræ have been found, but the difficulties in interpreting the differences have been great. The facts as they appear to the writer will now be presented.

Variation in the Number of Vertebræ from Sample to Sample.

Adopting some arbitrary standard of counting, including or excluding the urostyle according to choice, the "number of vertebræ" for each fish in a sample may be determined, and a frequency table prepared which summarises the individual counts. In its simplest form this table will show the number of individuals having (x), (x+1), (x+2) . . . etc. vertebræ respectively, but it is a simple mathematical operation to reduce the original numbers to a percentage basis, as if the sample really consisted of exactly 100 fishes. The percentage-frequencies may also be presented graphically, plotting the values of (x), (x+1), (x+2) . . . etc., as abscissæ and the corresponding percentages as ordinates. Alternatively, recognised statistical methods may be followed for the calculation of the "arithmetic mean number of vertebræ" for a sample, together with the "standard deviation" and "standard error."

Whichever way one elects to summarise sample-data, whether as a table of frequencies, a graph of percentage-frequencies, or an arithmetic mean, one is free to make direct comparison between sample and sample and thus to establish the extent of agreement or disagreement. The circumstances governing a particular investigation will, of course, decide which form of summary is the most convenient to adopt for the purpose of comparison. Sample A may be found to differ from sample B by an amount a, but the *significance* of the difference a cannot be accurately assessed without much detailed information concerning the samples themselves.

The samples to be discussed were taken from the regions shown in the chart on p. 307. Details of these samples are to be found in Ford (**8**), and also in Table XIX at the end of this paper in p. 383, and we shall first consider the total range of variation in number of vertebræ for all the samples examined, irrespective of locality and time of capture, or the length, age and sexual condition of the fishes taken. The individual number of vertebræ varies from 53* to 58* and the arithmetic mean from 55·48* to 55·99*. Fishes with 55 or 56 vertebræ together account for 78 per cent or more of every sample, while those with 57 vertebræ only rarely exceed 20 per cent. Fishes with 54 vertebræ hardly ever number more than 2 or 3 per 100, while those with 53 or 58 are very uncommon indeed.

* These numbers do not include the urostyle. Throughout this paper, unless otherwise stated, the number of vertebræ, whether individual or as an average, is always exclusive of the urostyle.

Expressing the percentage frequency of each sample in the form of a graph, it is found that the shape of the graph varies between the extremes shown at the top and bottom of Fig. 7, with intermediates such as those indicated in the figure. The change in shape of the graph is clearly due to the fact that the percentage of fishes with 55 vertebræ which is so dominant in sample A becomes progressively reduced (see also Fig. 8),

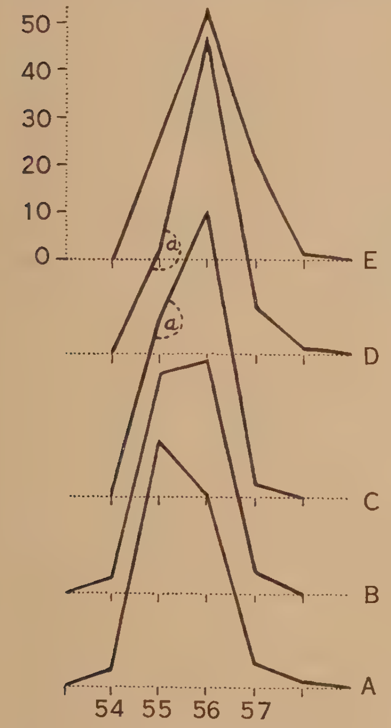

Fig. 7.—Five percentage frequency graphs of the number of vertebræ, representative of the range of variation in form.

A . . . Sample from statist. region VIIg. July, 1926.
B . . . „ „ Mounts Bay. March, 1926.
C . . . „ „ Brighton. December, 1926.
D . . . „ „ Plymouth. February, 1925.
E . . . „ „ statist. region VIIg. June, 1926.

In graph C, the angle a is less than 180°.
In graph D, the angle a is more than 180°.

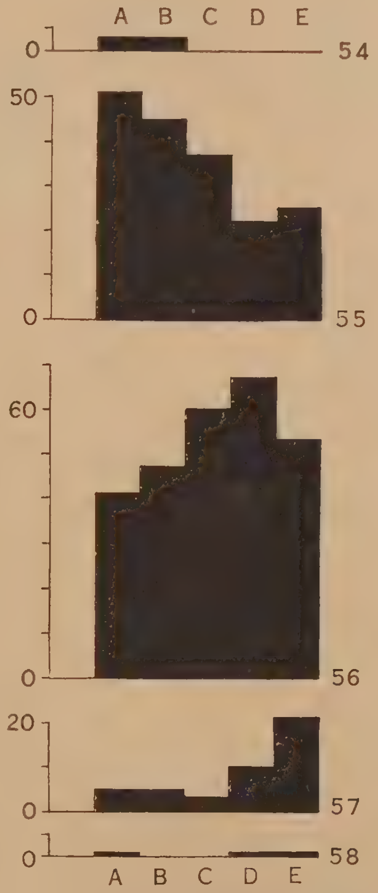

Fig. 8.—Percentage frequency in vertebral number for samples A to E. (See also Fig. 7.)

while the percentage of fishes with 56 vertebræ is increased. The percentage with 57 vertebræ increases from sample A to sample E.

Schnakenbeck (**29** and **30**) has strongly advocated the extensive use of percentage-frequency graphs of the kind shown in Fig. 7, and it is not denied that a pictorial representation of percentages will conveniently and plainly convey to the mind the composition of a sample with regard to the number of vertebræ. But when graphs of the "single-peaked" type, such as C and D in Fig. 7, are superimposed one above the other, an artificial "sameness" in appearance is apt to be created which may mask considerable differences in vertebral composition. For detailed comparison of frequency-graphs, therefore, some description criterion of "shape" would seem to be desirable. This is particularly needed when dealing with the present samples, the majority of which give the single-peaked type of graph. The following arbitrary* standards have been adopted :—

Class 1.

Percentage of fishes with 55 vertebræ is greater than that of fishes with 56 vertebræ. The frequency graph is illustrated by A in Fig. 7.

Class 2.

Percentage of fishes with 56 vertebræ is greater than that of fishes with 55 vertebræ, but the difference does not exceed 10%. The frequency graph is of the "truncated" type illustrated by B in Fig. 7.

Class 3.

Percentage of fishes with 56 vertebræ exceeds that for fishes with 55 vertebræ by more than 10 %, although it is less than twice the percentage for 55 vertebræ. Fishes with 57 vertebræ account for not more than 13%. Graph C in Fig. 7 belongs to this class.

Class 4.

Percentage of fishes with 56 vertebræ is at least twice that for 55 vertebræ. Percentage with 57 vertebræ is not more than 13%. In graphs of this class, represented by D in Fig. 7, the angle a is greater than 180°, whereas in graphs of class 3, angle a is less than 180°.

Class 5.

Percentage of fishes with 57 vertebræ is at least 14%, while the percentages for vertebræ 55 and 56 may agree with those of class 3 or 4. The frequency graph is typified by E in Fig. 7.

---

* It should be understood that the classification is quite arbitrary and artificial, and is used merely as a convenient standard for the purpose in hand.

The total of 103 samples examined may thus be split up according to the above five classes :—

Class 1	1
Class 2	7
Class 3	30
Class 4	53
Class 5	12

It is seen that the bulk of the samples falls into classes 3 and 4, indicating that fishes with 56 vertebræ are usually in decided predominance. But this segregation of samples according to vertebral distribution proves to be a segregation according to the geographical regions in which the samples were taken. This is shown in Table X :—

TABLE X

Region.	Number of Samples according to Vertebræ-Class.					Totals.
	1	2	3	4	5	
VIIe. (Sussex coast)	–	–	8	–	1	9
VIIe. (Brixham and Exmouth)	–	–	5	3	–	8
VIIe. (Plymouth area)	–	2	10	37	1	50
VIIe. (Mevagissey)	–	–	–	2	–	2
VIIe. (Mounts Bay)	–	1	–	2	–	3
VIIg. (Between English and Irish coasts southward of 52°N.)	1	3	1	4	10	19
VIIf. (Port Isaac Bay)	–	1	6	5	–	12
Totals	1	7	30	53	12	103

It will be observed from Table X that the samples from region VIIg and VIIe (Sussex coast) are different both from one another and from those of other areas. Of the 19 samples from VIIg no less than 10 are of class 5, as against only 2 of this class in the 84 samples taken elsewhere. Furthermore, only 1 of the VIIg samples is of class 3, whereas in VIIe (Sussex coast) 8 out of the total of 9 are of this class. In other words, samples from the Atlantic end of the English Channel (region VIIg) are characterised by a higher number of vertebræ than samples from the eastern end of the Channel (region VIIe, Sussex coast).

The majority of the Plymouth samples fall into class 4 which is intermediate in character between classes 5 and 3. But, geographically, Plymouth occupies an intermediate position between VIIg and VIIe (Sussex coast). Similarly, the Brixham and Exmouth samples are intermediate between those from Plymouth and Sussex, and so, also, are the geographical positions.

This tendency for the number of vertebræ to rise from east to west in the English Channel has been shown in an earlier paper (Ford, **8**) by using the arithmetic means for the samples, instead of the percentage-frequencies.

Although in region VIIg samples of class 5 are so much in evidence, it is in this same region that samples of classes 1 and 2 are the most common. Hence, in one and the same region, there is wide variation in the number of vertebræ. Although somewhat less pronounced, the range in vertebral variation in the other regions is also considerable. While, therefore, there is a tendency for the number of vertebræ to rise from east to west in the English Channel, there is wide variation between samples taken in close proximity to one another.

The Conception of " Races " of Herrings.

Having noted the extent of the differences in number of vertebræ between samples, it is helpful to enquire how such sample differences might conceivably be brought about. It is generally believed that the number of vertebræ, once fixed in the early life of an individual, remains unaltered, so that the difference in vertebral number between *samples* of fish must be due to the manner in which fish group themselves during the successive phases of their life-history. The *shoal*, as usually conceived, is a naturally formed group of herrings composed of individuals which differ in age but do not vary greatly in length or swimming capacity. But for how long a given shoal retains its distinctive identity without becoming merged into a greater entity or split up into groups, it is difficult to say. Nor is it easy to determine at what rate the composition of a shoal is changed as the result of the replacement of older members by recruits. Yet such changes might conceivably result in marked changes in vertebral distribution. Consider a spawning shoal arriving at a spawning place. It will show a certain vertebral distribution, and, presumably, will have all its members in approximately the same state of sexual maturity. If that shoal spawned by itself, we should have a parental spawning population of given vertebral distribution giving rise to a new generation. More probably, however, the spawning stock will consist of more than one shoal. Nevertheless, the vertebral distribution of the total spawning population might still remain fixed at a certain value provided that each and every shoal showed the same vertebral distribution. If such were the case, it is logical to think that the shoals which leave after spawning would also be alike in vertebral distribution, even if the retiring shoals were quite different as regards their individual members from those which came to spawn. The conceivable contrast is that of a complex spawning population made up of a number of shoals which differ in vertebral distribution, and of retiring shoals for which the vertebral distribution is different from that of the ones which contributed to the spawning population.

On a feeding ground, as opposed to a spawning ground, the only character in common which it is necessary to attach to individual shoals is that all have come to feed. It is of little moment that they may differ in vertebral distribution. But later on, when the call of spawning occasions the concentration of fish prior to a movement inshore to the spawning place, the facts are otherwise. If smaller shoals join forces to form greater ones there arises the possibility of the coming together of " groups " of herrings which have hitherto been distinct in their number of vertebræ, unless there be some inherent character in the fishes which impels them to make a deliberate choice of their associates for spawning. In this event, the period when shoals concentrate for the spawning migration could be regarded as a " sorting-out " time when genotypes come apart.

This brings us face to face with all the problems associated with the hypothesis of " races " in the herring. In his important theses, Schnakenbeck (**29** and **30**) considers the division of the herring species into a number of races which are to be regarded as morphologically and physiologically distinct entities. He suggests that each race is characterised by its number of vertebræ, which can be expressed in the form of a distinctive frequency graph. Members of a race spawn at a given time of year in given places, the continuity of the race from generation to generation being preserved by the strict inheritance of the number of vertebræ and by the fact that no two races spawn on the same ground at the same time.

If the basic premises for this conception of herring races were proven facts, it would be permissible to treat all samples of catches as race-samples, of which some might be homogeneous in race but others mixtures of races. Differences between samples would thus be manifestations of differences in racial composition. Indeed, this has been done already by Schnakenbeck himself who has postulated two distinct races within the geographical area covered by the Plymouth data. He includes all the herrings of the English Channel in one race, " The Channel Sea Herring," but refers those of the Smalls to a second race, designated " The Smalls Herring." Reserving judgment as to the validity of the premises on which Schnakenbeck has established these races, it is instructive to treat the Plymouth samples as if they were race-samples.

The " Channel Sea Herring " and the " Smalls Herring."

From Schnakenbeck's Fig. 33 (**30**, p. 516), which is here reproduced as Fig. 9 on p. 352, the form of the frequency graph typifying the number of vertebræ for the two races may be seen. It must be noted, however, that Schnakenbeck's count of the vertebræ is always one vertebra greater than the Plymouth count, since he includes the urostyle. Series A to the left of the figure represents the " Smalls " race, and series B on the right, the

"Channel" race. Reference to Schnakenbeck's legend to his Fig. 33 shows that the samples of Series A are actually the class 5 samples from region VIIg already referred to above, while it is evident from the figure itself (reproduced here as Fig. 9) that the Series B are class 3 samples from region VIId and e. The vertebral frequencies which Schnakenbeck uses as types of the races is given in p. 550 of his paper (**30**) :

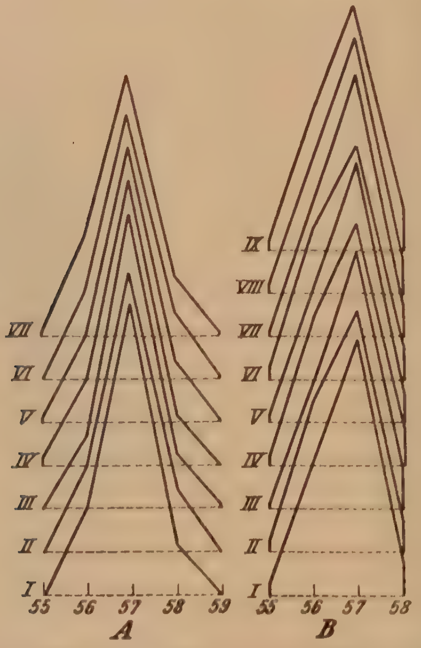

FIG. 9.—Reproduction of Fig. 33 from Schnakenbeck (**30**).

Series A.....Samples from "Smalls," region VIIg.
Series B.....Samples from Eastern English Channel.

	Number of Vertebræ.				
Schnakenbeck's count	55	56	57	58	59
Ford's count	54	55	56	57	58
"Smalls" race	–	20	64	14	1
"Channel" race	3	31	59	7	–

Here again it is seen that the vertebral frequency is of class 5 for the "Smalls" race and class 3 for the "Channel." The difference between these two frequencies and their graphic representation is so pronounced that no one will question their separation, even if doubts are retained as to their racial significance.

But since samples of classes 5 and 3 occur in other regions, it would seem necessary to stipulate that fishes of the "Smalls" race (or some other race having a similar vertebral frequency) may occur at Plymouth and even to the eastward of Plymouth as far as off the Sussex coast, and also that fishes of the "Channel" race (or another race having a similar vertebral frequency) are to be found off Exmouth and Plymouth and in the western regions VIIf and g. The inevitable conclusion from this is either that there is an extensive overlap in the range of distribution for the two races named, or that races other than the "Smalls" and the "Channel" are represented in the samples. The same difficulty arises if we accept the findings of le Gall (**17**), who some years ago distinguished between "Hareng type Atlantique, variété côtière" inhabiting the Channel proper, and "Hareng type Atlantique, variété du large" which were confined to deeper water and included the fish trawled at the Smalls and elsewhere in region VIIg.

But all the samples taken within the area of investigation are not of classes 5 and 3 alone. There are the samples of classes 1, 2 and 4 to be considered, and each region presents difficulties on this account. In regions VIIf and g, in Mount's Bay and at Plymouth, samples of classes 1 and 2 occur for which the vertebral frequency graph is quite unlike that of either class 5 or class 3. Schnakenbeck has remarked on this (**30**, p. 516) and definitely excluded them from his two main races. Perhaps the greatest difficulty arises, however, when we come to consider the samples of class 4, for which the vertebral frequency graph is of a form intermediate between those of classes 5 and 3. How are they to be interpreted? This question is of especial import in the Plymouth area where 37 out of the total of 50 samples belong to this class. Why in this area where the shoals are unquestionably assembled for spawning should there be such a dominance of samples which differ in vertebral distribution from the type-distributions characterising the "Channel" race and the "Smalls" race? If, as Schnakenbeck suggests (**30**, p. 518), the great majority of the Plymouth herrings in the winter months belong to the same race (i.e. the "Channel" race) as the herrings of the eastern Channel one would have expected close agreement in number of vertebræ between the majority of the Plymouth samples and those from off the Sussex coast. Instead, it is found that the Sussex samples are almost entirely of class 3, those of class 4 being absent, whereas at Plymouth class 4 samples outnumber those of class 3 by nearly 4 to 1. It will be necessary in a moment to note the degree to which the "number of vertebræ" for a sample of class 4 differs from that of a sample of class 3, but even if the difference were but slight, the fact remains that there *is* a difference, and that the Plymouth samples as a rule contain fewer fishes with 55 vertebræ and more than 56 than is shown by the Sussex samples. If, then, the "Channel" race actually exists, which are the purer samples of the race, those from Plymouth or those from Sussex? Furthermore, how does the difference between samples of class 3 and class 4 arise?

As a step in the study of these questions let us determine the extent of the difference between the vertebral distribution shown by the Plymouth samples and those from Sussex, restricting attention to those of classes 3 and 4. In the following Table XI samples are tabulated according to the percentage of fishes with 55 and 56 vertebræ respectively, in the form of a correlation table. The data relating to Sussex samples of class 3 are shown in the bolder clarendon type, those relating to Plymouth samples of class 3 are in italics, while the plain numbers refer to Plymouth samples of class 4:—

TABLE XI

NUMBER OF SAMPLES ACCORDING TO PERCENTAGES OF FISHES WITH 55 AND 56 VERTEBRÆ.

Percentage of fishes with 55 vert.	Percentage of fishes with 56 vertebræ.																				Totals.		
	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71			
20																				1	–		1
21																			2		–	–	2
22																1			1		–	–	2
23													1								–		1
24													1		2	1					–	–	4
25									1	1	1	1				1					–	–	5
26										1			1	2				1				–	5
27										3			2		1	1					–		7
28												1		1									2
29							1		2		1											–	4
30											1		1									–	2
31									**1**	*1* **1**		1									**2**	*1*	1
32						**1**		*1*			1										**1**	*1*	2
33									*1*												–	*1*	–
34				*1*					*1*													*2*	
35	*1*	*1*		**1**				*1*													**1**	*3*	
36																					–	–	
37		**1**	**1**			**1**			**1**												**4**		–
38																					–		
39					*1*																–	*1*	
40																					–		
41																						–	
42		*1*																				*1*	
Totals	–	**1**	**1**	**1**	–	**2**	–	–	**2**	**1**	–	–	–	–	–	–	–	–	–	–	**8**		
	1	*2*	–	*1*	*1*	–	–	*2*	*2*	*1*	–	–	–	–	–	–	–	–	–	–		*10*	
	–	–					1	–	3	5	4	3	6	3	3	4	–	1	3	1			37

Sussex samples of class 3 are shown thus : **1**
Plymouth ,, class 3 ,, ,, ,, *1*
Plymouth ,, class 4 ,, ,, ,, 1

It is seen from Table XI above that there is very little overlap between the Sussex samples of class 3 and the Plymouth samples of class 4. Whereas the former show from 31–37% of fishes with 55 vertebræ and from 53–61% of those with 56 vertebræ, the latter show from 20–32% with 55 vertebræ and from 58–71% with 56 vertebræ. On the other hand, the class 3 samples from the Sussex coast agree very well with the class 3 samples from Plymouth.

There appear three possible explanations of this definite difference between the Plymouth and the Sussex samples :—

1. The Sussex samples are "pure" samples of the Channel race, whereas the Plymouth samples are mixtures of Channel and some other race.
2. The Plymouth samples are "pure" samples of the Channel race, whereas the Sussex samples are mixtures of races.
3. Both the Sussex and the Plymouth samples are mixtures of races.

There is evidence from other sources that, at the eastern end of the English Channel and entrance to the North Sea, samples of herrings vary considerably in vertebral character. Thus, le Gall (**19**, p. 254), dealing with the French fisheries, has had to divide his area into three regions, in each of which the herrings differ in number of vertebræ. In the region southward of the Somme, from that river to Cap Antifer, the herrings are assigned to "Groupe II," for which the number of vertebræ as determined by samples during the past few years is as follows :—

	Percentage number of Vertebræ.					
le Gall's count . .	54	55	56	57	58	59
Ford's count . .	53	54	55	56	57	58
1928	—	0·9	29·3	59·1	10·1	0·4
1929	0·2	1·2	30·7	57·7	9·9	0·2
1930	—	0·6	30·8	61·8	6·8	—

Fishes of this "Groupe" are regarded as of a distinct "Channel" race, and it is seen that they conform very closely with Schnakenbeck's figures. It is also worth noting that the number of vertebræ on average tends to be on the low side as compared with the Plymouth samples of class 4. Thus, the percentage of fishes with 56 vertebræ does not amount to 62%, while the percentage with 55 vertebræ is not less than 29% (cf. Table X on p. 349).

Le Gall's second region is to the northward of the Somme between Cap Griz-Nez and the Somme, and the herrings are here referred to "Groupe I" : —

	Percentage number of Vertebræ.					
le Gall's count .	54	55	56	57	58	59
Ford's count . .	53	54	55	56	57	58
1928	1·2	3·4	44·4	45·8	5·2	—
1929	—	2·5	35·3	55·3	6·7	—
1930	0·2	1·8	35·0	56·4	6·3	0·2

There is in this group more variation. It is seen that by comparison with the classification used in this paper, the 1928 analysis is of our class 2, while those of 1929 and 1930 are of our class 3. Le Gall regards these as varying admixtures of two races, namely, his " Channel " type and " The Southern North Sea " type, the latter being mainly confined to the Southern North Sea, and characterised by an average number of vertebræ lower than that of the Channel type. His " Southern North Sea " type would show a frequency graph of the " truncated " type somewhat similar to those given by our classes 1 and 2.

Le Gall's third group is the " Groupe Dyck-Sandettié," coming from the region Dyck–Sandettié–Ruytingen, and captured mainly in the trawl :—

	Percentage number of Vertebræ.						
le Gall's count	54	55	56	57	58	59	
Ford's count	53	54	55	56	57	58	
1928	0·8	2·5	35·3	55·3	6·7	0·2	
1929	0·3	4·5	43·7	47·3	3·8	0·1	(also 0·3 less than 53 vert.)
1930*			39·0*	52·7*	6·5		

Here again, le Gall is led to regard these samples as mixtures of the two races named above, for it is impossible to assign them to either one or the other.

Le Gall has thus been able to interpret his results only by extending the range of the " Channel " race into the North Sea and introducing North Sea fish into the Channel. Tesch (**35**), in his investigations of young herrings in the southern sea entrances of Holland, and of adult herrings from the southern North Sea and the eastern part of the English Channel, also finds it necessary to assume considerable overlap in range between races of the North Sea and those of the Channel, even going so far as to suggest " kinship " between the young fish from the Ooster-Schelde and the Plymouth fishes.

Gilson (**21**), too, investigating the Belgian fishery for " spent " herrings between Ostende and Cap Gris-Nez, obtained counts of vertebræ which cannot be reconciled with a single race.

Leaving the eastern end of the Channel to return to the Plymouth samples, it cannot be said that the samples show any greater tendency to conform to type than those in the localities just dealt with. Some of the Plymouth samples could be referred to the " Channel " race, but there remain others which could not, either because the number of vertebræ is too low (class 2 samples) or because it is too high (samples of class 5 and a proportion of those of class 4). If races exist, then the Plymouth samples provide evidence of race mixture.

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* There is an obvious error in the setting up of this table in the original, but the figures given appear to be the correct interpretation.

Summarising the conclusions reached in this section, it appears that :—

1. Not all the samples from VIIg conform with the " Smalls " race.
2. Not all the samples from the Plymouth district conform to the " Channel " race.
3. Not all the samples at the eastern end of the Channel conform to the " Channel " race.
4. The number of vertebræ tends to be higher in samples from the Atlantic end of the Channel than in those from the eastern end, although there is an appreciable range of variation in the sample-averages in each region investigated.

Samples from Plymouth and District.

Seeing that the Plymouth district is an important spawning ground, it is just here that one would most expect to obtain pure race samples. Furthermore, since spawning fishes may occur at Plymouth from the end of September until late in the spring, there would seem to be reasonable time for more than one race to spawn without overlap. But as the Plymouth samples were not specifically collected as part of a " race " enquiry, it is, perhaps, hardly surprising that they do not prove very satisfactory for this latter purpose. The majority of them are heterogeneous in the sense that they are composed of fishes which vary in the condition of the gonads, and none of them are sufficiently large to warrant the breaking-up into components.

There is some evidence, however, for believing that in the year 1925, fishes with a comparatively low number of vertebræ spawned within Plymouth Sound from the end of September until the beginning of November. On the nights of September 30th, October 8th, and November 1st, stop-nets set in the Sound beneath the Laboratory took catches which included a number of spawning fish, and on October 25th a drift-net catch in Cawsand Bay also included spawners. Further evidence of this local spawning was afforded by the capture of " spent " fish in the Tamar estuary on November 20th. The low number of vertebræ characterising these samples is exemplified by the following results :—

Date. (1925).	Locality.	Percentage number of Fishes with number of Vertebræ as follows : 54	55	56	57	58
October 25th	Cawsand Bay . .	3	42	53	3	–
November 1st	Below Laboratory . .	1	45	50	5	–
November 20th	Tamar Estuary . .	–	39	56	4	–

In the following year, 1926, a sample from the Sound below the Laboratory on October 21st, and samples from Cawsand Bay on October 18th and 25th included a few spawners, although not so many as in the previous year. Of these three, the Cawsand Bay sample of October 18th showed a low number of vertebræ, but the remaining two did not :—

Date. (1926).	Locality.	Percentage number of Fishes with number of Vertebræ as follows : 53	54	55	56	57	58
October 18th	Cawsand Bay . .	–	–	46	47	7	–
October 21st	Below Laboratory .	–	–	28	63	8	1
October 25th	Cawsand Bay . .	1	3	23	64	10	–

Samples taken on the open drifting grounds outside Plymouth Sound during October and November in 1925 and 1926, were composed entirely of " full " fishes at maturity-stages IV and V. Only one of these samples, namely that taken in East Bay on November 18th, 1925, showed a vertebral distribution comparable with the low values given by the samples from the Sound and Cawsand Bay. The remainder included a higher proportion of fishes with 56 vertebræ :—

Date.	Locality.	Percentage number of Fishes with number of Vertebræ as follows : 53	54	55	56	57	58
November 4th, 1925	Whitsand Bay . .	–	1	24	67	8	1
November 18th, 1925	East Bay . . .	–	2	35	59	5	–
November 3rd, 1926	Off Looe . . .	–	–	28	65	7	–
November 4th, 1926	Off Rame Head . .	–	–	27	64	9	–
November 15th, 1926	Rame–Eddystone .	–	2	27	61	10	–
November 23rd, 1926	Rame–Eddystone .	1	1	29	62	7	–

Putting these facts together, there may be some justification for suspecting that in October and November, fishes which are low in number of vertebræ spawn in the neighbourhood of the Sound. But, outside the Sound on the usual drifting grounds, shoals are present which are not yet ready to spawn and which have a higher number of vertebræ. The difference in vertebral character between these two kinds is shown graphically in Fig. 10, the " flat-topped " graphs applying to the early spawners.

In contrast with this, it has been found almost impossible to make a similar separation of samples taken during December, January and February, when the main fishery is in progress. Considerable spawning occurs all the time, but vertebral distribution appears to vary without relation to the stage of maturity. In Table XII, data are given for ten samples, selected because they each consist for the most part of fishes in the spawning condition, i.e. at maturity-stage VI :—

TABLE XII

Sample.	Percentage number of Fishes with number of Vertebræ as follows : 54	55	56	57	58	Arithmetic Mean No. of Vertebræ.
1	2	34	55	8	1	55·72
2	1	32	62	4	–	55·70
3	2	31	61	5	1	55·72
4	–	30	62	8	–	55·77
5	1	29	60	10	–	55·80
6	2	27	61	10	–	55·79
7	–	27	64	9	–	55·83
8	2	24	64	10	–	55·82
9	–	23	63	14	–	55·91
10	1	20	71	8	–	55·86

Comparison between samples shows :—

1. The percentage of fishes with 55 vertebræ varies between 34% and 20%
2. ,, ,, ,, ,, 56 ,, ,, ,, 55% ,, 71%
3. ,, ,, ,, ,, 57 ,, ,, ,, 4% ,, 14%
4. The arithmetic mean no. of vertebræ varies from 55·70 and 55·91.

The differences between the samples is thus quite considerable, and yet all of them consisted mainly of spawning fishes. That is to say, it is hardly permissible to regard the samples as representative of one and the same race, unless the differences in vertebral composition are overlooked. Nor as an alternative, is it any easier to accept the vertebral differences as evidence of the presence of, say, two races, for this would mean that two races must be spawning together on the same grounds at the same time.

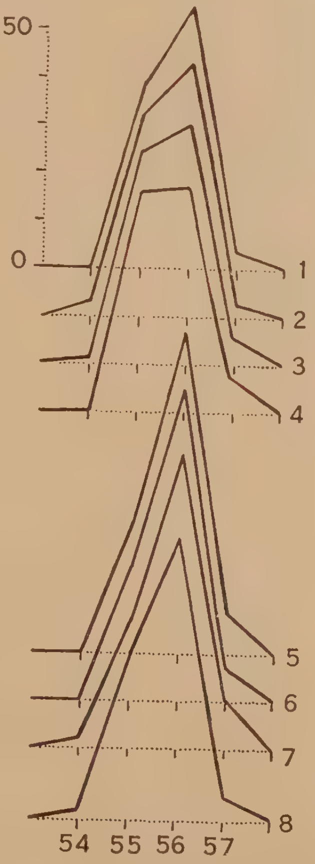

Fig. 10.

Percentage frequency graphs of number of vertebræ.

1. R. Tamar, November, 1925.
2. Cawsand Bay. October, 1925.
3. Sound. November, 1925.
4. Cawsand Bay. October, 1926.
5. Whitsand Bay. November, 1925.
6. Off Looe. November, 1925.
7. Rame–Eddystone. November, 1925.
8. Bigbury Bay. November, 1925.

Vertebral Variation among Spawning Fishes.

In an endeavour to obtain fuller knowledge concerning the variation in the number of vertebræ among fishes spawning together, two larger samples of actually spawning fish were analysed during January, 1931. To obtain the first of these samples, the writer proceeded to Sidmouth in Devon, where the chances of obtaining spawners in the requisite quantity appeared to be most favourable. On January 6th, a drift-net catch of several thousands was landed, and as soon as possible after landing, a start was made in the process of going through the catch, fish by fish, gently squeezing the abdomen to determine whether or not ripe eggs could be expressed. All the fishes which had thus been proved to be females fully ripe for spawning were retained, and a total of 355 individuals was collected before the catch must needs be packed for transport. It may be explained that the restriction of the sample to females only was largely a matter of convenience. It is well known that at maturation the eggs become translucent and the ovaries lose their firmness—eggs escape easily from the body in response to slight pressure, giving a sure indication of ripeness. In the case of the males, there is not that certainty in distinguishing ripe from unripe—or so it appears to the writer.

The sample having been forwarded to Plymouth, the length of each fish was determined, the age was read from the scales, and the number of vertebræ in the cleaned skeleton was counted. In reading the age from the scales, some disappointment was felt when it was found that by no means every fish could be referred with certainty to a definite year-group. Since it was undesirable to reject any part of the sample on this account, additional age-classes had to be created so that every fish would be included in the final summary of age.

The sample as a whole and in its age-components gave the following results :—

TABLE XIII

	Number of Fishes in each of the following Vertebræ-Classes :							
Age-Group.	54	55	56	57	58	Abnormal Skeletons.	?	Total Counts.
?	–	–	1	–	–	–	–	1
2	–	1	2	1	–	–	–	4
3	–	32	51	2	–	4	1	85
3 or 4	–	14	35	3	–	–	–	52
4	1	24	36	9	–	2	1	70
4 or 5	–	6	10	4	–	1		20
5	–	11	31	8	1	4	–	51
5 or 6	–	4	11	2	–	–	–	17
6	1	9	16	3	–	–	–	29
6 or 7	–	1	4	–	–	–	–	5
Older than 6	–	5	1	1	–	1	–	7
Total Sample	2	107	198	33	1	12	2	341

Although the numbers of fishes in the separate age-groups are not as large as could be wished, the following calculations of arithmetic means and errors serve their purpose in demonstrating that the vertebral distribution is subject to appreciable variation :—

Age Groups.	Total Number of Fishes.	Arithmetic Mean Number of Vertebræ.	Standard Error of Mean.
Whole sample	341	55·777	·067
Younger fishes (Age-groups 2, 3, 3 or 4)	141	55·709	·046
Older fishes (Age-groups 4 or 5, and all older groups)	129	55·860	·060
3	85	55·647	·057
5	51	55·980	·095
5 and 6	80	55·900	·078

Whether or not these differences in average number of vertebræ may be considered significant is shown by the results of tests of independence given in Table XIV :—

TABLE XIV

Age Groups compared. I	with II	Arithmetic Means. M_2	M_1	Difference. (M_2-M_1)	Standard Error of Difference.	Ratio : $\frac{\text{Difference}}{\text{Standard Error.}}$
5	3	55·980	55·647	0·33	0·11	ca. 3
5 and 6	3	55·900	55·647	0·25	0·096	$>$ 2
whole sample	3	55·777	55·647	0·13	0·067	ca. 2
5	whole sample	55·980	55·777	0·20	0·10	ca. 2
Older fishes	Younger fishes	55·860	55·709	0·15	0·075	ca. 2

From these results one is at least justified in hesitating to regard the total samples as "homogeneous" in vertebral distribution. The fishes of age-group 3 appear not to agree with those of age-group 5, or with those of groups 5 and 6 taken together, and younger fishes do not agree with older ones. Recalling that every fish in this Sidmouth sample was a fully-mature female, ready to spawn if not actually doing so, it is difficult to escape the conclusion that the spawning population sampled was a mixed assembly of fishes which differed in vertebral distribution from age-group to age-group.

The second sample came from a total of about one thousand herrings caught by s.s. *Salpa*, using the otter trawl in Bigbury Bay on January 14th, 1931. With the assistance of four colleagues at the Plymouth Laboratory, a total of 623 fishes from this catch were subjected to an analysis of length, sexual condition, age and number of vertebræ. In all, 439 individuals were ripe (Stage VI), while the remaining 184 included "full" fishes at stage V, and "spents" at stage VII.

It was found that the male fish were generally shorter in length than the females :—

Sex.	Stage of Maturity.	Length Classes (cm.) 21	22	23	24	25	26	27	28	29	30	Mean Length Male.	Female.
♂	VI	–	–	2	3	13	74	103	64	17	2	27·45	
♀	VI	–	–	–	1	2	29	66	47	13	3		27·79
♂	V	–	–	–	1	5	28	33	17	7	1	27·42	
♀	V	–	–	–	–	2	15	24	15	5	1		27·65
♂	VII	1	–	–	1	1	–	3	1	–	–	26·07	
♀	VII	–	–	–	–	2	4	4	5	6	2		28·15

Finding that the difference in length between male and female persisted even when age was also taken into account, it was decided to treat the sexes separately in the investigation of their number of vertebræ, as in Table XV :—

TABLE XV

	No. of Fishes in following Vertebræ Classes.					Arithmetic Mean No.	Total No. of
	54	55	56	57	58	of Vertebræ.	Fishes.
A. Whole Sample							
Males only	3	121	226	27	–	55·735	377
Females only	–	76	143	26	1	55·805	246
Both sexes	3	197	369	53	1	55·762	623
B. Fishes at Stage VI							
Males only	2	97	159	20	–	55·709	278
Females only	–	50	94	17	–	55·795	161
Both sexes	2	147	253	37	–	55·740	439
C. Fishes NOT at Stage VI							
Males only	1	24	67	7	–	55·808	99
Females only	–	26	49	9	1	55·823	85
Both sexes	1	50	116	16	1	55·815	184

It is clear from Table XV that the females were not only of a greater average length, but had a higher average number of vertebræ. The male fish at maturity stage VI gave interesting results. Of the total of 278, no less than 142 were old fishes exceeding the age of 6 zones, 6 rings, and having the following number of vertebræ :—

No. of Vertebræ	54	55	56	57	58
No. of Fishes	1	56	77	8	–

Arithmetic Mean No. of vertebræ = 55·648
Standard Error of Mean = 0·050

The male and female fish at maturity stage VI thus gave the following averages :—

	Arithmetic mean No. of vertebræ.
" Old " Males	55·648
Other Males	55·772
Females	55·795
All	55·740

Statistical test shows that the difference of 0·147 vert. between the mean for the old males and that for the females can hardly be attributed to chance. This being so, not much significance can be attached to the actual value of the arithmetic mean number of vertebræ for all the fishes of stage VI taken together. Thus, as was the case with the Sidmouth sample, there is reason to doubt whether the spawning population sampled was really homogeneous in vertebral character.

It cannot be claimed that the results given by these two samples definitely prove that spawning populations may be mixed in vertebral character, but they certainly demonstrate that just as much care is needed when comparing samples which are homogenous in sexual condition as is demanded when samples are not homogeneous in that respect. It is seen that the arithmetic mean number of vertebræ for the total Sidmouth sample of spawners is almost the same as that for the spawners among the Plymouth sample. The samples were taken within a few miles of each other and at practically the same date. Everything thus appears to favour the view that fishes belonged to a single stock. But the analysis of the samples has shown that it is doubtful whether, under the circumstances, the means for the samples as a whole can be legitimately compared at all.

Herrings of the "O" Group.

The number of vertebræ of the offspring from a spawning stock is a matter of importance. Many counts of vertebræ in samples of late post-larval and metamorphosing herrings have been made at Plymouth, and large differences have been observed. Two facts have been recorded (Ford, **14**, p. 748) concerning the number of vertebræ in samples taken from neighbouring estuaries during 1927 and 1928 from April until June:—

1. The number of vertebræ tended to be higher in later months.
2. Within the same day's sampling, the number of vertebræ changed with the length of the fishes.

The extent of the difference which may be shown between samples taken at different times is exemplified by the data for samples taken on May 26th, 1927, and April 5th, 1928:—

	Body-length* Distribution.		Vertebral Distribution.				
	30 mm.	35 mm.	54	55	56	57	58
April 5th, 1928 .	50	49	2	41	46	10	–
May 26th, 1927 .	51	50	–	3	58	38	2

The very high number of fishes with 57 vertebræ in the sample of May 26th may occasion some surprise, as this does not usually much exceed 10% in samples of adults at Plymouth. The correspondingly low number with 55 vert. is also unusual. The data given, however, have been confirmed by the counting of a second sample. Perhaps a more typical case is provided by a comparison between the above sample of April 5th, 1928, and one taken on May 18th of the same year, and even here the difference is self-evident:—

	Body-length Distribution.		Vertebral Distribution.				
	30 mm.	35 mm.	54	55	56	57	58
April 5th, 1928 .	50	49	2	41	46	10	–
May 18th, 1928 .	55	50	–	14	70	11	–

The second feature, that of difference in vertebral distribution within one and the same sample, is exemplified by samples taken on May 27th and June 25th, 1928 (Ford, **14**, p. 749). In the May sample, fishes less than 35 mm. in body-length had a higher average number of vertebræ than those exceeding 35 mm., while in the June sample, fishes from 50 to 55 mm. had a higher average than those from 60 to 65 mm.

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* The "body-length" is equivalent to the total length less the caudal fin. Defects in the caudal fin of many specimens necessitated the use of this alternative method of expressing length (*vide* Ford, **10**, p. 307).

The Sample and the Race.

The various forms of investigation described above agree in showing that in an attempt to use the " number of vertebræ " given by random samples as a clue to the racial composition of the populations sampled, there is the persistent difficulty of apparent race-mixture. This leads us to enquire into the validity of the basic proposition that the number of vertebræ as given by a sample can be accepted as an estimate of a race character. For convenience in writing, we will refer to the sample estimate as the " sample-number " and to the race character as the " race-number."

Having determined a large number of sample-numbers, an investigator may decide to place some of them in a group apart from the rest *because they agree.* He may make a special note of the absolute value of the number of vertebræ which is characteristic of the members of the group he has created and decide to establish this as a " type " to which future samples of the same vertebral composition may be referred. But this " type " is nothing more than a quite arbitrary standard, and the " constancy " with which the members of the group conform to type is solely the result of the deliberate exclusion of samples which differ from standard. The mere sorting-out of sample-numbers into types according to a criterion of vertebral distribution of itself proves nothing beyond the fact that a certain number of the samples are alike in their number of vertebræ, but differ from others in this respect. It is simply and solely a technique for the assessment of the amount of variation in vertebral distribution.

Alternatively, the investigator may first segregate his samples according to some character *other than the number of vertebræ*, only to find that in one of the resulting groups all the samples also agree in vertebral distribution. In this instance the agreement between the " sample-numbers " is not merely the result of a deliberate choice of sample according to an arbitrary standard of vertebral distribution, but a sequel to a selection of samples according to some other criterion. It shows, moreover, that there is a correlation between the character used for the sorting of the samples and the number of vertebræ.

The fundamental difference between the above two alternatives is self-evident, but it needs to be remembered in the present discussion of " sample-numbers " and " race-numbers." Were it proven that the principle of "race-numbers" is valid, the first alternative would be a legitimate method for conducting racial analyses, but unless and until that principle is established, the results of such analyses remain entirely speculative. By the adoption of the second of these alternatives and paying due regard to the sexual condition of the fishes in the samples he utilises, Schnakenbeck has accumulated a wealth of valuable information which he offers as substantial evidence for the "race-number." Certainly, he has shown that sexual condition and "sample-number" are interdependent, but it is a matter of opinion as to whether or not he has proved either that the number of vertebræ is strictly inherited, or that spawning populations are homogeneous in vertebral composition—and these two premises are the fundamental elements of the theory of unalterable "race-numbers."

Without more knowledge than is at present available concerning the inheritance of the number of vertebræ, there must remain some uncertainty as to the real significance of observed difference between "sample-numbers." There is at least the possibility that some part of this difference is phenotypic—a possibility which may increase the difficulty of using "sample-numbers" as "race-numbers" in seeking to establish genotypes. This explains the present writer's hesitation in accepting the system of herring races postulated by Schnakenbeck, or, at the present time, to proceed further with a racial analysis of the Plymouth samples than has been indicated in the foregoing pages. It may well be that Schnakenbeck has in broad outline already mapped out the different races as they actually exist, and that his technique is basically sound, but he has given no proof.

Until this proof is forthcoming, it is held that "sample-numbers" should be treated merely as characters of the temporary populations from which the samples are drawn and not as "race-numbers." They can be used in conjunction with data on age and growth as clues to the movements of the shoals which result in the formation of those temporary populations, and persistent work of this kind ought ultimately to reveal the different entities represented in the populations. The Scottish investigations on the autumn-spawning and spring-spawning herrings in Scottish waters provide an excellent example of the application of this method.

Concerning the Plymouth spawning population, there remains no doubt that it is very complex. Whatever character is considered, it is found that the Plymouth fishes have something in common with those taken in regions to the eastward and westward. Just as some of the Plymouth fishes are indistinguishable in growth from those caught at the eastern end of the Channel, while others resemble those taken in the Atlantic fisheries, so also there is a relation between the "sample-number" of vertebræ in the three districts. On the whole, also, growth in length in western regions tends towards a higher limiting value than that in eastern regions ; similarly, the number of vertebræ tends to rise from east to west. Many of the Plymouth herrings exhibit " mixed " growth, suggesting that in the seasons between successive spawnings they have visited different feeding grounds ; so, too, the number of vertebræ varies from sample to sample, as if to confirm the belief that the Plymouth spawning population is drawn from a number of different sources. The explanation which seems best to fit these results is that the shoals which arrive in succession to spawn off Plymouth come both from the deeper parts of the English Channel proper and from the more open waters at the Atlantic entrance. After spawning, they return to off-shore waters, although not necessarily to the same grounds from which they came. Accepting the view that the Plymouth spawners spend the whole of their lives within a fairly definable and comparatively limited geographical area, and that the number of spawning places is also limited, it might be permitted to speak somewhat loosely of a " south-western " herring which differed, say, from a Norwegian herring. Nevertheless, there will be marked individual variation among " south-western " fishes in both growth and number of vertebræ, since the size of annual increments of growth depends upon the feeding grounds visited when fishes are a given age and size, while the number of vertebræ, although in a measure dependent upon the parental number, may yet be affected by the environmental conditions under which fishes are born and develop.

The Rearing of Young Herrings.

Great advance in our knowledge of genotypes in herrings might be expected if it were possible to rear herrings of known parentage under controlled conditions. In practice it is a comparatively simple process to express eggs from a ripe female and to fertilise them with the milt from a ripe male. The eggs thus " set " will develop quite normally in sea-water and give a plentiful yield of active and apparently strong larvæ. No special care is needed to secure this result other than that usually taken in the experimental rearing of marine animals. Whenever opportunity has permitted at Plymouth, eggs have been fertilised and incubated until larvæ have appeared. Eggs have been incubated in plunger-jars ; in running water and still ; in the light and in the dark ; in water of different temperature and salinity. Unfortunately, however, no larvæ have ever been reared much beyond the stage at which the yolk-sac is absorbed, and it has become increasingly evident that the problem of rearing cannot be treated as an incidental to other enquiries if success is to be achieved. It must be undertaken as a major research. As an aid in this it was thought that Plymouth could assist by acting as a distribution centre for fertilised eggs and supply workers in laboratories elsewhere, where facilities for rearing are available.* Thanks to the co-operation of Mr. Storrow at Cullercoats ; Professor Orton of Liverpool University, and Mr. Smith of Port Erin ; Mr. Elmhirst of Millport ; and Mr. Weller of the Municipal Aquarium at Brighton, trial consignments were sent to the above places and reports made on subsequent incubation. Ripe eggs were expressed from females into glass jars (breffits) partly filled with water, the jars being moved about meanwhile so as to distribute the eggs as evenly as possible in a single layer over the inside of the jar. The eggs were then fertilised by pouring into each jar a small quantity of a suspension of sperm in sea-water. After fertilisation had been effected, the water was changed. Two breffits containing eggs and securely capped with glass covers and muslin, were packed in a hamper and despatched by rail to each of the four Laboratories mentioned. The hampers for Brighton, Cullercoats and Millport left by passenger train, and that for Port Erin went first to Liverpool by rail and was then transferred to the steamer for Douglas in the Isle of Man. Upon arrival at their destination, the eggs were housed according to the facilities available. Excellent hatchings were reported.

The Number of Myomeres in Larval Herrings.

Being unable to rear larval herrings of known parentage until the number of vertebræ could be counted, an attempt was made to determine how the number of myomeres varied, but with equally disappointing results. It is well known that an error of one or two in the counting of myomeres is unlikely to lead to a mistaken identification of a herring as distinct from a sprat or a pilchard. But no such latitude in precision of count is permissible when studying myomeral variation within a herring brood—the counts must be reliable statistics—and in practice there was no assurance on this important point. It is thought, however, that with opportunity for closer investigation, interesting results might be forthcoming.

Incubation of Herring Eggs in Waters of different Salinities.

Despite the failures referred to above, it has been shown (Ford, **13**) that fertile eggs of the same parentage can be made to yield larvæ which differ in specific gravity as the result of incubation in waters of different salinities. This opens up the question as to what anatomical variation, if any, might be expected to reveal itself in the fishes at a later stage of life, in consequence of this difference in environment during embryonic development. At present, nothing further can be added to the original report.

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* There is, of course, nothing very new in this. As early as 1879, Dunn (**4**) forwarded some thirty or forty thousand eggs to the Brighton Aquarium in connection with a proposal to "enrich Australian waters with the English Herring," and he states that whereas full ninety days was required for the journey with the transported eggs still unhatched, it was found possible to "repress life" for only forty days. In later years, ova fertilised at Plymouth were the material for trial transportation to New Zealand, and were successfully taken as far as Cape Town.

The Metamorphosis of the Herring.

Leaving the larva and turning to the stage in the life of a herring when it becomes transformed into a silvery and scaled adolescent, there is considerable variation to be explained. The marked changes in form during metamorphosis can be regarded as the consequences of differential growth in length (Ford, **14**) and it is suggested that any circumstances which will affect the relative proportions of the different parts of the larval body, or which will influence the rate at which these different parts grow, must induce a difference in the form of the adolescent. It has been shown that at Plymouth the length at which metamorphosis occurs is by no means constant, and that early larvæ at an arbitrary stage of metamorphosis are larger and have a lower number of vertebræ than those at the same stage of transition in later months. To what extent these changes are genotypic or phenotypic remains to be determined.

The Adult Fish.

After the adolescent, there is the adult fish. Whether it has grown much or little ; whether it has matured early or late ; whether it agrees with or differs from a second fish in its number of vertebræ : there remains the ever-present difficulty regarding the interpretation of differences between individual herrings.

Technique.

It remains to speak of the technique by which the investigator seeks to recognise genotypes in the herring. Stated simply ; he has to devise means for distinguishing between fishes which differ in factorial constitution. The manner in which he essays to solve the problem is immaterial, provided that his method is reliable. The " number of vertebræ " is a character much used in this connection, but it appears that there is still much to learn about this character. In a communication to the *Journal du Conseil*,* now in the press, the present writer has discussed the " number of vertebræ " as the sum of a series of bony elements which differ one from the other. Two individuals may have the same total number of vertebræ, but yet be different in the structure of the vertebral column. Reference must also be made to an important paper by Wollaston (**39**), recently published, in which the statistical treatment of sample data on the number of vertebræ is most critically examined.

* *Journal du Conseil*, Vol. VIII, No. 2, 1933.

FORECASTING THE YIELD OF THE FISHERY.

It would be of practical advantage to the fishing industry if, at some time in advance of the opening of a new season's fishing, fishing prospects could be announced with regard to the following :—

(*a*) The date when profitable fishing might be expected to begin.
(*b*) The expected quality of the catches.
(*c*) The estimated yield of the fishery.

If events during the fishing season were repeated year after year with unbroken regularity, knowledge during any one season would be quite sufficient to indicate what would happen in the next. We know, however, that no such uniformity actually occurs. Even so, if it could be shown that the variation from season to season followed some rule, it might yet be possible to discover that rule from the study of past data, and hence to predict what is likely to occur in the future.

Is there any " law and order " governing the whole or some part of the fluctuations in fishing yield which can be discovered from the study of past data on the Plymouth fishery ? Is there any certainty that future events will continue to follow the same course ? Until positive answers can be given to these questions, any forecasting is pure speculation, and therefore without scientific value.

It can be regarded as certain that fishing results are dependent upon the weather, but in the present state of meteorological science, we cannot hope to receive much advance information regarding weather conditions during a forthcoming season. Hence, every form of fishery forecast which can be issued at the present time must of necessity include an important reservation dealing with the weather. Nevertheless, the official weather forecasts which are broadcast daily are themselves in the nature of fishery predictions. Thus, a gale warning is not solely an indication that an interruption of fishing is imminent, but also a portent of heavy catches when fishing is resumed after the enforced suspension. Alternatively, the prediction of a spell of calm weather may be interpreted as an indication of lighter catches. It is certain that a detailed study of the relation between weather and fishing yield will form an important part of future work on fishery prediction.

But however favourable the weather may be for fishing, the size and number of catches made are dependent upon the fish stocks. There is reasonable assurance that some fish, at any rate, will be found on the grounds as early as October, and that not until at least the end of January will it be possible to say that none can be caught in drift-nets. Moreover, during the intervening four months the condition of the fish will vary from individuals with half-filled roes and milts to fish which have spawned. But beyond these two general statements, it is almost impossible to be sure of anything except that the quantity and quality of fish caught varies from season to season, day to day, and from boat to boat, in a bewildering fashion.

It is believed that the fish come in successive shoals, partly from the English Channel proper and partly from the neighbouring Atlantic waters. After spawning, the fish will return once more to the deep. Year after year this inshore migration for spawning, and the return journey to the offshore feeding grounds, is repeated. An observer at Plymouth, therefore, by studying samples of fish taken during the winter fishery, can obtain a working idea of the changes which occur from one season to the next. He sees how the stock alters in character by the gradual replacement of older fish by younger; how that fishes born in a given year outnumber those born in other years; and he learns to distinguish between fishes which have come from different feeding grounds. From these detailed studies, conducted over a number of years, he finds that he can formulate an empirical cycle of events which will, to a useful degree, account for the observed changes in the fishable stock. Let us examine some of the results obtained in this way.

On p. 325 data were given on the age of fishes caught during the seasons 1924–25 to 1931–32, and it was there shown (1) that fishes born in certain years were much more important to the fishery than those born in others; and (2) that fishes of any given year-class are of the greatest importance to the fishery in their fifth winter of life. Now these are observations which, strictly speaking, refer only to the period in which they were noted. That is to say, there is no certain proof that they will apply at some future date. On the other hand, there is no real necessity to assume that they will not. Accordingly, there can be no objection to the experiment of attempting to forecast the age-composition of catches during a future season on the basis of past observations. In the year 1929, an experiment of this kind was made, utilising data taken during the four seasons 1924–25 to 1927–28. (*vide* Ford, **11**, p. 14.) It was predicted that the rich year-class 1923 would begin to decline in 1928–29 and that in its stead the very successful 1925 year-class would predominate in the catches of 1929–30. Furthermore, dates were given when year-classes 1922 to 1925 would cease to be important elements in the catches, and the opinion was expressed that by 1932–33 practically the whole of the stock represented in the catches of 1927–28 would be replaced by new stock. Concerning these experimental predictions it is now possible to say from actual experience that they were substantially correct. Since this first attempt it has been the custom at the end of each season to form an opinion as to the probable age-composition of the catches in the following year, and it may be said that there has been no fundamental discrepancy between forecast and fact.

It may not appear of great practical utility to be able successfully to forecast the age composition of catches, nor is there any value in so doing, if the work is to stop at this point. But if it is remembered that as a fish gets older it increases in size, then it will be realised that a forecast of age-composition is also a forecast of "quality" of catch. For example, if catches during an impending season are expected to include a high proportion of old fish it means that big fish will outnumber small. Conversely, the prediction of a high percentage of young fish in future catches is only another way of saying that the average size of the fish will be small. But at Plymouth this is merely a generalised truth, for it is at present very difficult, if not impossible, to convert predictions of age-composition into precise predictions of size quality, because fishes of the same age group vary considerably in size. Of course, a high average age usually means a high average size, but an individual length is no criterion of age any more than an individual age is a criterion of length (cf. p. 326). Size will depend upon the feeding grounds which the fish have frequented in past years, so that the average size of the fishes taken during any season at Plymouth will depend upon the regions from which the shoals have come. And in the present state of knowledge there is little justification for assuming that each year sees an unaltered proportion of migrants from the Channel proper and from the Atlantic regions. If in some years there is a greater proportion of migrants from the Atlantic feeding grounds the average size for any given year class is likely to be larger than in the years when the Channel migrants are in greater evidence. The winter of 1932–33 provides a case in point. From the observations made during the preceding season it was anticipated that the catches of 1932–33 would include a high proportion of old fishes, since there had been no important replenishment of stock by younger year classes in recent years. At the same time it was felt that unless the brood of the winter of 1929–30 had proved very successful in its survival the outlook for the fisheries of the immediate future was very disquieting. Now if these anticipations were to become realised facts the catches of 1932–33 should have shown an appreciable percentage of fishes of the larger sizes, as well as a fair quota of small individuals—the former being the old fishes remaining from previous stock and the latter the new arrivals of the young 1929–30 brood. Fishes of medium size, representing fishes from 4 to 6 years of age, should be few in comparison. These results were actually obtained during the fishery, but in a manner which was not, and could not have been foretold. Old fishes certainly predominated in the catches of 1932–33, so much so that samples taken from catches in several instances consisted of from 50% to 80% of individuals over the age of 6 years, whereas the average percentage for fishes over 6 years during the previous eight seasons was only 25%. With so large a percentage of old fish it was quite according to expectation that the average size of the fishes in the catches should also be large, but it came as a surprise to see *how* large they really were. Individuals of 28 cm. to 30 cm. in length outnumbered others, while those from 25 cm. to 27 cm. were less in evidence than in perhaps any year since 1924–25. The explanation which most satisfactorily accounts for this fact is that shoals coming from the Atlantic regions were more numerous than in recent years.

Young fishes of the 1929 30 season made their appearance in a very marked manner during the months of September, October and November, 1932. During that period catches were landed at Plymouth and at a number of places off Cornwall which included anything from 30% to 60% of the 3-year-old fishes of this year-class. The frequency and the characters of these fishes were altogether unusual, at least in the Plymouth area. They were of large average size in comparison with fishes of the same age usually caught at Plymouth, being about 25 cm. long on average. But more noticeable still, they had a much higher average number of vertebræ than is usual in the district. Fishes having 57 vertebræ actually outnumbered those with 55 vertebræ, and the average number of vertebræ exceeded 56·0 in four out of the five samples taken from Plymouth landings. Such high vertebræ averages are not ordinarily obtained in Plymouth waters and can only be matched by averages in the Atlantic region VIIg. (*vide* p. 349). Samples from Mevagissey and Port Isaac, taken during the same period, showed very similar characters, and it seems most natural to conclude that these and the Plymouth fish were of like origin.

From these observations it would appear that the fishable stock on the Plymouth grounds during the 1932–33 season had come more from westerly sources than had been the case for a number of years. But this change was not predictable because there was no available evidence upon which to judge. Hence, although a knowledge of the age-composition of catches in previous years proved sufficient to prepare a forecast of the age-composition in 1932–33 there was no means of expressing more than a generalised opinion on the probable size-quality of the catches. In other words, the prediction of a high percentage of old fish implied that the average size would tend to be high, but it was impossible to state that the fishes would be mostly 28 cm. to 30 cm. in length, because it could not be foreseen that the shoals would be predominately westerly in character.

For the same reason there is at present a limitation to the accuracy with which forecasts of the *quantity* of fish can be given. As will be indicated below, extremely useful general indications as to the quantity of fish to be expected can be extracted from analyses of past records, but these are all dependent upon the underlying assumption of unaltered conditions between present and future. Four times out of five, or perhaps nine times out of ten, that assumption may be sufficiently near to the truth, but at the fifth or the tenth time it may fail. For example, a marked alteration in the migration of herrings such as is thought to have occurred during 1932–33 might well upset any prediction of quantity which did not take into account the possible effects of the migratory change. As to the causes which might induce these migratory changes, it has been suggested that the cyclic activity of Atlantic waters is one of the most important. Thus Storrow (**34**, p. 20) says : "In the study of fluctuations of the herring fishery we are confronted with the problem of associating changes in fisheries with changes in waters, and these with changes in other phenomena such as the association of pressure distribution and winds." French investigators (*vide* le Gall, **20**) have gone so far as to associate the fluctuation of the herring fisheries in the English Channel with rhythmic movement of Atlantic water over the Continental plateau, and to predict the success or failure of the fishery in consequence of this rhythm. Many will think, however, that our knowledge of the factors which govern the movements of herring shoals has not yet reached that stage when it can be used in the practical forecasting of fishing yield. But the fact remains that such knowledge will have to be sought after, despite the complexity of the problems awaiting solution.

But even if the significance of these unknown factors governing the movement of shoals is admitted, there is much to be learned from past results of actual fishing. In Table IV, on p. 315, the average weight per landing by steamers at Plymouth during each of the seasons 1924–25 to 1931–32 was given. Using these figures as the best available estimate of density of catch, and placing them alongside the corresponding age-composition of the catch, we have the following material for study :—

	Season.							
	1924–25	1925–26	1926–27	1927–28	1928–29	1929–30	1930–31	1931–32
Average weight per steamer-landing (cwt.)	**40·0**	23·1	16·6	**46·3**	27·5	**39·1**	32·7	17·6
Age composition of catches expressed as percentage-numbers of fishes of following year-classes :—								
1919 . . .	15·3							
1920 . . .	**56·0**	**47·5**						
1921 . . .	12·3	14·1	10·7					
1922 . . .	7·0	15·2	22·9	12·0				
1923 . . .		**5·3**	**27·9**	**30·9**	**26·6**			
1924 . . .			4·7	20·4	19·5	15·4		
1925 . . .				**18·6**	**30·8**	**35·9**	**33·2**	
1926 . . .					3·3	18·1	23·8	21·3
1927 . . .						1·9	10·2	15·0
1928 . . .							4·4	12·6
1929 . . .								3·4

It will be seen from the above table that there is a relationship between the density of steamer-landing and the percentage-number of fishes in the three year-classes 1920, 1923 and 1925. The steamer-landing was heaviest in the three seasons 1924–25, 1927–28 and 1929-30, and in these same seasons the most important part of the catch consisted of fishes of 1920, 1923 and 1925 year-classes, respectively, when those fishes were at the age of 5 years. In 1926–27 and 1931–32, the steamer-landing was very low, and it was in just those seasons that fishes of the above-mentioned year-classes were comparatively weakly represented. Thus, in 1926–27, the year-class 1920 had reached the age of 7, so that the time had passed when it might be expected to make a heavy contribution to catches. Moreover, the 1923 year-class was only aged 4, and therefore not yet yielding its full quota, while year-class 1925 was not due to appear in the catches until the following year. In 1931–32, all three classes had passed their zenith—it is probable that those of 1920 and 1923 were little more than nominally represented in the catches, if at all, while that of 1925 had reached its maximum two seasons previously. The data further show that the fishery from 1924-25 onwards has depended far more upon year-classes 1920, 1923 and 1925 than upon any others.

Putting these observations together, there seems good reason for thinking that the yield of the Plymouth fishery (as represented by the average weight per steamer-landing) fluctuates in accordance with the strength of a limited number of highly-successful year-broods, occurring only at intervals. The yield will reach a maximum when one of these rich broods is in its fifth winter. It follows from this that the moment an observer can learn of the arrival of a new and successful brood, he is in the position to forecast when fishing is likely to benefit from that event. Thus, when in the season 1927–28 the present writer (Ford, **11**, p. 16) noted that the percentage of 3-zoned 3-ringed fishes of the year-class 1925 was unusually high, he could have gone on to predict that the fishery in 1929–30 would be good. And the prediction would have been realised, although made two years in advance.

The converse case must also be noted, for if during successive seasons no evidence is forthcoming that an important new brood is about to take the place of those passing out of the fishery, then it must be concluded that the fishery will suffer in consequence. In this connection it is of interest to consider the progress of the Plymouth fishery during the past four seasons (1929–30 to 1932–33). In 1929–30, when fishes of the rich year-class 1925 at the age of 5 years made up 35·9% of the catch, the average steamer-landing was 39·1 cwt. During the following season of 1930–31, fishes of the same year-class, now 6 years old, were again dominant, but the average weight per steamer-landing fell to 32·7 cwt. In 1931–32 the steamer yield was lower than it had been since 1926–27, while the catches consisted of no less than 47·7% of fishes older than 6 years. These results plainly show that fishes of year-classes 1926, 1927, 1928 and 1929 were not present on the Plymouth grounds in anything approaching the density with which those of year-class 1925 had been. There are two ways of explaining these results. Either the broods of the winters 1925–26 to 1928 29 were poor in survival-rate as compared with that of 1924–25, or the four former broods did not visit Plymouth to the same extent as did the latter brood, but went elsewhere to spawn. Of the two explanations, the first appears the more likely since there is independent evidence that the dominance of the year-classes 1920, 1923 and 1925 was widespread (*vide* Storrow, **33** and **34**).

The position at the end of the 1931–32 season at Plymouth, therefore, appeared anything but favourable for the fishery of 1932–33. What remained of the previously fished stock was old, while there was little to be expected from the oncoming younger broods. The only possible prediction which could be made was that the fish of the 1932–33 seasons would consist of a greater proportion than ever of old fish, and that the average yield would be low. As has already been shown, the proportion of old fish did prove to be exceptionally high, but it has to be noted that the average weight per steamer-landing was considerably heavier than might have been expected. Yet it must be said that this discrepancy between forecast and fact was more apparent than real because, unfortunately, the average of 34·2 cwt. per steamer-landing does not convey a fair estimate of the season's fishing. On p. 318 it was shown that fishing was only really productive during two periods, the first from December 7th to December 18th, and the second from January 4th to 6th. Admittedly, during the 12 days of the first period and the 3 days of the second, the steamer-landings were very good, averaging 53 cwt. per landing (and this good result has been shown to have been dependent upon good fishing weather), but there were 36 other days during the season when the steamers were far less successful, and for which the average is only 20 cwt. as compared with the 9-year seasonal average of 30·8 cwt. The results of the motor fishery tell a similar story, for whereas there were 12 days on which the average weight per landing was equal to or greater than the seasonal average of 20·2 cwt., there were 27 days when the daily average was much below this figure. For the 12 days the average weight per landing was 36·5 cwt., but for the 27 days it was only 11·6 cwt., and there were an additional 17 days when no landings at all were made. Thus, when some two-thirds of a working season gives decidedly poor results, too much significance ought not to be attached to a seasonal average like the weight per steamer-landing which, in effect, spreads the heavy landing of a few days over a long period of poor yields. The result, as in the present instance, is apt to be misleading.

From these observations it may be concluded that although the average weight per steamer-landing fluctuates from season to season in accordance with the changing age-character of the fishable stock, its limitation as a precise estimate of fishing yield creates some difficulty in forecasting future results. It will therefore be necessary for prediction purposes to find some better criterion of the density of fishing.

Now it is a self-evident fact that forecasts of quality and quantity which are determined in the manner just described are concerned only with the expected remains of previously-fished stock. They have nothing to do with that entirely fresh stock which enters the fishery for the first time in any one year. At Plymouth there is at present no means of anticipating the strength of the 3-year-old stock in an impending season, but this is of little practical consequence because the proportion of 3-year-old fishes in the catches is relatively unimportant. Elsewhere, however, where the catches always include a high proportion of 3-year-old stock (off the Sussex coast, for example), it would be necessary to discover some means of determining the relative richness of an oncoming year-class before it had reached its third year as well as to obtain an indication of the expected yield from previously-fished year-classes.

There remains to be considered the question of the time at which fishing in any season may be expected to begin. This matter of early and late seasons was given some attention in an earlier paper (Ford, **11**) when it was suggested that the temperature of the sea may provide a clue. It was found that at temperatures above 13°C. fishing tended to be poor, but that it improved as the temperature fell towards 11°C. and became good as soon as the temperature was less than 11°C. The "normal" date at which 11°C. is reached is about December 19th. An individual season would thus be early or late in starting according as the temperature of 11°C. is attained before or after the "normal" date. It has not been possible to examine this question in further detail, but it is worth noting that on December 6th, 1932, the temperature over the Bigbury Bay area of the fishing grounds was round about 11°C. and on the next day, December 7th, the steamers made the first big landing of the season. This suggests that the matter may be worthy of more critical and detailed investigation.

Having reviewed the present possibilities and limitations connected with the general question of predicting catches, it is convenient to consider available data in somewhat greater detail. The average age-composition of catches during the eight seasons from 1924–25 to 1931–32 was given in Table VI on p. 325, and at the foot of that table the following means for the 8-year period were stated :—

Percentage Numbers of Fish at following Age:

3	4	5	6	Older than 6
6·1	18·4	27·3	22·7	25·3

The figures are seen to increase from the 3rd to the 5th year, but to begin to decline in the 6th. Assuming that the decline is continuous from the 6th year onwards at a fixed rate of about 54% annually, the percentages at ages 7, 8 and onwards may be estimated as follows, making the total percentage of fishes older than 6 amount to 25·4 instead of 25·3 :—

Percentage Numbers of Fish at following Age :				
7	8	9	10	11
12·3	6·6	3·9	1·9	1·0

The above may be regarded as representing the "normal" life of a year-class *in the fishery*, and suggests that this life commences with a minor contribution at the age of 3 years, growing to a maximum at 5 years, and dwindling to a merely nominal representation from the age of 8 years onwards.

This hypothetical "life-table" is not only useful in giving an estimate of the length of time and the extent to which the fishery may be expected to profit or suffer by the presence of a "normal" year-class, but also in showing the manner in which oncoming year-classes must increase their quotas in order to make good the losses sustained by the passing out of the older classes. It is seen that of the nine year-classes which contribute to the catch of any one season, only those at the ages of 3 and 4 will increase their contributions during the next season, whereas the seven classes at the ages of 5 to 11 will contribute less than hitherto. Hence, if in actual experience a numerically weak year-class enters the fishery, its weakness will be almost immediately reflected in the density of the catch, while the effect upon the catch of two weak year-classes in succession will be very apparent. Conversely, the arrival of a rich year-class will lead to an early rise in the catch.

TABLE XVI.

Season.	Percentage by Weight contributed by Year-classes at the following Age :					
Dec.–Jan.	3	4	5	6	Older than 6	
1924–25	5·6	11·7	55·8	15·7	11·3	
1925–26	3·9	13·4	13·4	49·1	20·2	
1926–27	4·2	24·2	21·8	11·3	38·5	
1927–28	14·9	18·6	32·0	12·9	21·6	
1928–29	2·6	27·6	19·4	27·7	22·7	
1929–30	1·5	16·0	34·7	15·9	31·8	
1930–31	3·5	9·4	22·8	33·3	31·0	
1931–32	2·8	10·6	13·8	21·7	51·1	
Average	4·9	16·4	26·7	23·4	28·5	Total=99·9%

When one comes to consider the density of actual catches in relation to their composition by age, there is the difficulty that the catches are expressed in terms of either volume (crans) or weight (cwt.), whereas the age composition is given in numbers. Since no actual data are available as to the weight of fishes at different ages (and such would be difficult to obtain in practice), the alternative has been adopted of obtaining a working idea of the age-composition of catches, *by weight*, by assuming that weight is proportional to the cube of the length and then calculating the weight of fishes at different ages from the corresponding lengths. Table XVI, on page 377, is thus an expression by weight of the numerical age-composition given in Table VI, on p. 325.

Dividing up the average weight per steamer-landing according to the above percentages, season by season, we obtain the following :—

TABLE XVII.

Season.	Average weight per steamer-landing. (cwt.)	Weight of Fish at following Age (cwt.).				
		3	4	5	6	Older than 6
1924–25	40·0	2·2	4·7	22·3	6·3	4·5
1925–26	23·1	0·9	3·1	3·1	11·3	4·7
1926–27	16·6	0·7	4·0	3·6	1·9	6·4
1927–28	46·3	6·9	8·6	14·8	6·0	10·0
1928–29	27·5	0·7	7·6	5·3	7·6	6·2
1929–30	39·1	0·6	6·3	13·6	6·2	12·4
1930–31	32·7	1·1	3·1	7·5	10·9	10·1
1931–32	17·6	0·5	1·9	2·4	3·8	9·0
Average	30·4	1·7	4·9	9·1	6·75	7·9
%	99·9	5·6	16·1	30·0	22·2	26·0

With the seasonal catch thus split up into age-components, it becomes possible to estimate how much the fishery depended upon the three year-classes 1920, 1923 and 1925 :—

TABLE XVIII.

Season.	Average weight per steamer-landing. (cwt.)	Weight of Fish of following Year-classes.				
		1920	1923	1925	Total.	Percentage.
1924–25	40·0	22·3	–	–	22·3	56
1925–26	23·1	11·3	0·9	–	12·2	53
1926–27	16·6	3·5*	4·0	–	7·5	45
1927–28	46·3	3·0*	14·8	6·9	24·7	53
1928–29	27·5	1·0*	7·6	7·6	16·2	59
1929–30	39·1	·5*	6·7*	13·6	20·8	53
1930–31	32·7	·3*	4·0*	10·9	16·2	50
1931–32	17·6	·2*	2·0*	4·9*	7·1	40

It is thus estimated that in each season from 1924–25 to 1931–32, the year-classes 1920, 1923 and 1925 accounted for approximately one-half of the catch. A measure of the superior yield of these three classes is provided by comparing their quotas at the age of 5 and 6 when they were making their fullest contribution to the fishery, with the corresponding quotas of other year-classes :—

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* These values are estimates on the assumption that rate of decrease each year after the 6th is about 54% annually.

	Year-classes.						
	1920.	1923.	1925.	1921	1922.	1924.	1926.
Weight contributed to steamer-landing during 5th and 6th years	33·6	22·4	24·5	5·0	7·6	11·5	11·3

It is seen that the quotas contributed by the year-classes 1920, 1923 and 1925 were individually much in excess of those given by the classes 1921, 1922, 1924 and 1926. The largest quota, that of 1920, was over six times as great as the smallest, viz. that of 1921, while the quotas of 1923 and 1925 were each from four to five times the heavier.

With this measure of the inequality of the contributions to the catch made by successive year-classes, and the knowledge of the extent to which the density of the catch is dependent upon the contributions made by a limited number of year-classes, the chances of being able to predict the trend of future fishing would seem to be favourable, provided that it is possible to learn in advance which year-classes are the ones of promise. Looking over the results of the past eight seasons, one must conclude that a good year-class hardly makes itself evident in catches before it is in its fourth year, although the impending importance of year-class 1925 became evident when that class was at the age of 3. Nevertheless, this is one year's prior notice of an important influence upon the size of the catch. Earlier indication, however, may be forthcoming by the examination of catches taken during the months from September to November, when it is usual for local boats to land catches of younger fish. Certainly in the late autumn of 1932, fishes of year-class 1930 were particularly in evidence, and it is upon this class that one expects the fishery of the near future to depend in no small measure. Admittedly, they were not generally strong in the commercial catches of December, 1932 and January, 1933, although occasional catches were landed which included a good percentage of small fish, but if the year-class is to be as important as the October samples suggested, then the catches in 1933–34 should show an appreciable percentage of 4-year-old fish, while in 1934–35, this year-class, now in its fifth winter, should be a dominant element in the catches. Accordingly, the yield of the fishery should show a new and satisfactory maximum in 1934–35, subject, of course, to the reservations discussed above.

From these observations at Plymouth it has been concluded that the continuous study of the changes in the character and density of commercial landings provides clues to the size and quality of future landings, despite the fact that the results of a season's fishing so obviously depend to an appreciable degree on circumstances which cannot as yet be foreseen. The limitations of the average weight per steamer-landing as an estimate of the density of the fishable stock are large, but they do not mask the fact that fishing-yield fluctuates in accordance with the varying richness of successive year-broods. In practice it is possible to obtain advance information of the relative richness of broods and hence of the relative success of future fisheries. But there still remain possible influences which may militate against a forecast of yield based entirely on this evidence, chief among these being the factors which govern the migrations of herrings. These call for investigation.

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TABLE XIX.

Statistical Region	Fishing Ground.	Method of Fishing.	Port of Landing.	Date of Sample.	Percentage No. of fishes in 6 Vertebræ Classes. 53	54	55	56	57	58	Total No. of Fishes in sample (n).	Arith. Mean No. of Vertebræ (m).	Standard Deviation σ	Standard Error of m $\frac{\sigma}{\sqrt{n}}$
VIIg	“ Smalls ”	Trawl	Milford Haven	Aug. 19th, 1925	1	–	25	55	19	–	100	55·91	0·73	0·073
		,,		Sept. 1st, 1925	–	–	20	68	12	–	95	55·92	0·56	0·056
		,,	,,	Sept. 14th, 1925	–	–	17	69	13	1	144	55·97	0·58	0·048
		,,	,,	Sept. 30th, 1925	–	1	20	64	14	1	95	55·94	0·65	0·066
		,,	,,	Oct. 19th, 1925	–	–	21	62	16	1	140	55·97	0·63	0·054
		,,	,,	July 28th, 1926	–	1	43	46	10	–	90	55·64	0·68	0·076
		,,	,,	Aug. 10th, 1926	–	2	34	52	11	–	96	55·73	0·69	0·070
		,,	,,	Aug. 18th, 1926	–	3	42	43	12	–	86	55·63	0·73	0·078
		,,	,,	Aug. 24th, 1926	–	–	31	50	18	1	98	55·90	0·72	0·073
		,,	,,	Sept. 2nd, 1926	–	–	26	55	20	–	97	55·94	0·67	0·068
		,,	Plymouth	Sept. 7th, 1926	–	–	20	65	15	–	112	55·955	0·59	0·056
		,,	Milford Haven	Sept. 28th, 1926	–	2	26	60	12	–	85	55·81	0·85	0·072
		,,		Nov. 15th, 1926	–	1	23	61	14	1	134	55·91	0·65	0·056
VIIg	Between English and Irish Coasts southwards of latitude 52° N.	Drift Nets	Newlyn	April 24th, 1926	–	1	20	60	17	2	96	55·99	0·70	0·072
			Milford Haven	April 26th, 1926	–	2	40	49	9	–	157	55·65	0·67	0·053
		,,		June 16th, 1926	–	–	23	62	14	1	126	55·93	0·63	0·057
		,,	,,	June 23rd, 1926	–	–	25	53	21	1	95	55·98	0·71	0·073
		,,	Newlyn	June 23rd, 1926	–	2	29	61	8	–	131	55·74	0·62	0·053
		,,	Milford Haven	July 13th, 1926	–	3	51	41	5	1	155	55·48	0·67	0·053
VIIf (ZZ 51)	Port Isaac Bay and Vicinity	Drift Nets	Padstow	Nov. 5th, 1925	–	2	20	66	12	–	119	55·88	0·61	0·056
			,,	Nov. 11th, 1925	–	1	29	65	5	–	118	55·75	0·56	0·051
		,,	,,	Nov. 17th, 1925	–	1	30	58	12	–	118	55·805	0·64	0·059
		,,	,,	Nov. 25th, 1925	–	–	31	63	6	–	118	55·75	0·56	0·051
		,,	,,	Dec. 11th, 1925	–	2	26	61	11	–	115	55·82	0·64	0·060
		,,	,,	Nov. 10th, 1926	–	1	32	60	7	–	111	55·75	0·60	0·057
		,,	,,	Nov. 16th, 1926	–	1	33	60	6	–	112	55·715	0·59	0·056
		,,	,,	Nov. 24th, 1926	–	3	38	50	9	–	116	55·66	0·68	0·064
		,,	,,	Nov. 29th, 1926	–	1	30	66	4	–	108	55·72	0·54	0·052
		,,	,,	Dec. 7th, 1926	–	–	33	58	9	–	106	55·76	0·61	0·059
		,,	,,	Dec. 20th, 1926	–	–	35	53	11	1	116	55·78	0·67	0·062
		,,	,,	Dec. 28th, 1926	–	2	43	44	11	–	110	55·645	0·70	0·067
VIIe (YY 52 & 53)	Mounts Bay	Trawl	Plymouth	Mar. 9th, 1926	–	3	45	47	5	–	113	55·55	0·64	0·060
		,,	,,	Mar. 17th, 1926	–	1	27	63	8	1	117	55·80	0·62	0·057
		,,	,,	Mar. 22nd, 1926	–	1	29	64	7	–	132	55·76	0·57	0·051
VIIe (ZZ 52)	Mevagissey Bay, 6 miles E.S.E. of Mevagissey	Set-Nets	Mevagissey	Oct. 26th, 1925	–	3	31	62	4	1	135	55·69	0·62	0·052
		Drift	,,	Jan. 8th, 1926	–	–	23	68	9	–	95	55·85	0·55	0·056
VIIe (ZZ 52 A 52)	Area covered by local fishery at Plymouth	Set-Nets Seine Drift Nets	Plymouth	Nov. 20th, 1924	–	1	27	67	5	–	115	55·77	0·55	0·051
			,,	Dec. 3rd, 1924	–	1	31	63	6	–	99	55·75	0·56	0·056
			,,	Dec. 9th, 1924	–	2	24	66	8	–	97	55·80	0·60	0·061
			,,	Dec. 16th, 1924	–	–	26	65	9	–	100	55·83	0·57	0·057
			,,	Jan. 5th, 1925	–	–	26	64	10	–	98	55·85	0·58	0·059
		,,	,,	Jan. 8th, 1925	–	2	27	61	10	–	100	55·79	0·64	0·064
		,,	,,	Jan. 13th, 1925	–	–	29	60	10	1	98	55·84	0·64	0·064
		,,	,,	Jan. 20th, 1925	–	–	23	63	14	–	99	55·91	0·61	0·061
		,,	,,	Jan. 27th, 1925	–	–	27	64	9	–	97	55·825	0·57	0·059
		,,	,,	Feb. 2nd, 1925	–	1	32	62	4	–	95	55·695	0·58	0·058
		,,	,,	Feb. 9th, 1925	–	–	25	63	12	–	99	55·87	0·60	0·060
		,,	,,	Feb. 18th, 1925	–	–	22	67	10	1	99	55·90	0·60	0·060
		,,	,,	Feb. 20th, 1925	–	–	34	60	6	–	97	55·72	0·57	0·058
		,,	,,	Mar. 2nd, 1925	–	2	25	67	6	–	97	55·77	0·59	0·060
		,,	,,	Oct. 25th, 1925	–	3	42	53	3	–	118	55·57	0·61	0·056
		,,	,,	Nov. 1st, 1925	–	1	45	50	5	–	107	55·58	0·60	0·058
		,,	,,	Nov. 4th, 1925	–	1	24	67	8	1	120	55·83	0·61	0·056
		,,	,,	Nov. 18th, 1925	–	2	35	59	5	–	107	55·66	0·59	0·057
		,,	,,	Nov. 20th, 1925	–	–	39	56	4	–	117	55·65	0·56	0·052
		,,	,,	Dec. 1st, 1925	–	2	25	60	13	1	117	55·86	0·65	0·060
		,,	,,	Dec. 6th, 1925	–	1	26	65	8	–	119	55·81	0·59	0·054
		,,	,,	Dec. 15th, 1925	–	1	30	64	5	–	115	55·74	0·56	0·052
		,,	,,	Dec. 21st, 1925	–	1	25	62	12	–	114	55·86	0·62	0·058
		,,	,,	Dec. 23rd, 1925	–	2	21	70	7	–	118	55·84	0·60	0·055
		,,	,,	Jan. 1st, 1926	–	–	32	59	8	–	118	55·76	0·59	0·055
		,,	,,	Jan. 6th, 1926	–	1	27	66	7	–	113	55·79	0·57	0·054
		,,	,,	Jan. 10th, 1926	–	1	29	60	10	–	118	55·80	0·62	0·057
		,,	,,	Jan. 14th, 1926	–	–	30	62	8	–	119	55·77	0·57	0·052
		,,	,,	Jan. 18th, 1926	–	1	27	61	11	–	114	55·825	0·63	0·059

TABLE XIX—*continued.*

Statistical Region.	Fishing Ground.	Method of Fishing	Port of Landing.	Date of Sample.	Percentage No. of fishes in 6 Vertebræ Classes.						Total No. of Fishes in sample (n).	Arith. Mean No. of Vertebræ (m).	Standard Deviation σ	Standard Error of m $\frac{\sigma}{\sqrt{n}}$
					53	54	55	56	57	58				
VIIe	Area covered by	Set-	Plymouth	Jan. 25th, 1926	–	2	22	70	6	1	116	55·83	0·59	0·055
(ZZ 52	local fishery at	Nets	,,	Jan. 28th, 1926	–	2	24	64	10	–	115	55·82	0·61	0·057
A 52)	Plymouth	Seine	,,	Feb. 2nd, 1926	–	–	24	66	9	1	110	55·87	0·59	0·056
		Drift	,,	Feb. 4th, 1926	–	1	20	71	8	–	115	55·86	0·54	0·051
		Nets	,,	Feb. 10th, 1926	–	–	20	70	10	–	117	55·91	0·54	0·050
		,,	,,	June 8th, 1926	–	3	29	58	10	–	92	55·74	0·68	0·071
		,,	,,	Oct. 18th, 1926	–	–	46	47	7	–	109	55·615	0·62	0·061
		,,	,,	Oct. 21st, 1926	–	–	28	63	8	1	113	55·81	0·61	0·057
		,,	,,	Oct. 25th, 1926	1	3	23	64	10	–	110	55·79	0·69	0·066
		,,	,,	Nov. 3rd, 1926	–	–	28	65	7	–	118	55·79	0·55	0·051
		,,	,,	Nov. 4th, 1926	–	–	27	64	9	–	112	55·82	0·58	0·054
		,,	,,	Nov. 15th, 1926	–	2	27	61	10	–	105	55·80	0·62	0·060
		,,	,,	Nov. 23rd, 1926	1	1	29	62	7	–	106	55·73	0·68	0·067
		,,	,,	Nov. 30th, 1926	–	–	33	60	7	–	118	55·74	0·58	0·053
		,,	,,	Dec. 6th, 1926	–	2	25	61	12	–	114	55·84	0·64	0·060
		,,	,,	Dec. 20th, 1926	–	–	26	61	12	1	107	55·88	0·64	0·062
		,,	,,	Dec. 20th, 1926	–	2	31	61	5	1	119	55·72	0·62	0·057
		,,	,,	Dec. 30th, 1926	–	3	35	52	10	–	119	55·70	0·69	0·063
		,,	,,	Dec. 30th, 1926	–	–	26	69	5	–	100	55·79	0·52	0·052
		,,	,,	Jan. 4th, 1927	–	2	34	55	8	1	112	55·72	0·67	0·063
		,,	,,	Jan. 19th, 1927	–	3	35	53	9	–	117	55·67	0·68	0·062
VIIe	River Dart	Seine	Brixham	Dec. 10th, 1925	–	1	33	55	11	–	97	55·76	0·66	0·068
(A 52)	Great West Bay	Set-	,,	Nov. 10th, 1925	–	1	22	67	9	–	76	55·84	0·59	0·068
		Nets	,,	Nov. 26th, 1925	–	2	32	56	10	–	116	55·72	0·67	0·062
		and	,,	Dec. 16th, 1925	–	1	30	63	5	–	92	55·73	0·58	0·060
		Drift	,,	Jan. 4th, 1926	–	–	38	50	12	–	64	55·75	0·66	0·083
		,,	,,	Oct. 27th, 1926	–	2	26	66	6	–	107	55·76	0·58	0·056
		,,	,,	Nov. 23rd, 1926	–	–	34	61	5	–	116	55·71	0·56	0·052
		,,	,,	Dec. 14th, 1926	–	2	37	56	5	–	119	55·65	0·61	0·055
VIId	Off Sussex Coast	Set-	Plymouth	Dec. 9th, 1924	–	2	27	55	16	–	98	55·86	0·70	0·071
(D 51		Nets or	Brighton	Oct. 19th, 1925	–	1	37	54	8	–	124	55·69	0·63	0·056
E 51)		Drift	,,	Nov. 10th, 1925	–	2	31	60	7	–	97	55·72	0·65	0·066
		,,	,,	Dec. 1st, 1925	1	3	37	53	5	1	118	55·62	0·72	0·066
		,,	,,	Nov. 1st, 1926	–	3	35	55	7	–	119	55·66	0·64	0·059
		,,	,,	Nov. 5th, 1926	–	1	31	61	7	–	97	55·74	0·60	0·061
		,,	,,	Dec. 2nd, 1926	–	–	37	60	3	–	97	55·66	0·54	0·054
		,,	Hastings	Dec. 10th, 1926	–	2	32	57	10	–	115	55·74	0·65	0·061
		,,	Brighton	June 29th, 1927	–	3	37	57	3	–	99	55·60	0·56	0·056

Observations on the Reactions of Marine Plankton to Light.

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With 22 Figures in the Text.

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FOREWORD.

That light is among the more influential elements in the environment of the smaller marine organisms is widely recognised. While laboratory investigation has revealed its kinetic action in specific ways, its capacity for stimulating behaviour responses, and its orientating action on directed movement, the observations of field-workers are providing a growing body of evidence that light does indeed act as an important factor in the bionomics of species in the wild.

The effect of changes in illumination on vertical distribution is an obvious case in point. Now, this line of investigation, as is characteristic of such marine ecological studies, deals essentially with the movement of populations, or groups. The sort of conclusion to be derived from the results is that changes in the distribution of a population correlate significantly with changes in illumination. In practice, it is usually possible to go beyond generalisations of this kind, but doing this involves assumptions concerning the behaviour of individuals composing the group. Indeed, the closer the correlation, the more necessary it becomes to think in terms of the behaviour of individuals. This is a general necessity in the study of populations which form quite unorganised groups, since the behaviour of the whole is merely a reflection of the units composing it.

Hence appears a demand for knowledge of the behaviour of individual plankton animals. Since, however, insurmountable difficulties exist in the direct observation of these animals in their natural habitats, there is little possibility of obtaining the required information other than by investigation in the laboratory. To offset the advantages of controlled experiment, laboratory conditions, always more or less restricted and unnatural, are particularly so in the case in point, and more than usual care has to be exercised in ascribing significance to results obtained under them.

Still, granted that the behaviour of a population is to be rendered intelligible by knowledge of what the individuals composing it are doing, and granted that the behaviour of individuals in the laboratory bears at least some kind of ascertainable relation to that of animals in the wild, it is concluded that data derived from the laboratory is not altogether without ecological value.

Turning now to what can be observed with regard to plankton animals confined in glass containers, one has to admit that the behaviour is, for the most part, featureless. There is little amongst the varied contrasts and changes to which the animals may be subject that can modify, or give added direction and coherence to their activity. Consequently, particular significance must be attached to any factor of the environment which exerts consistent marked effects. It so happens that light proves to be just such a factor. Sudden changes in light intensity may produce shock reactions as readily as mechanical contact, while the clustering on the lighted side of glass containers is familiar to all who have had anything to do with plankton. Since, in the laboratory, the behaviour is perhaps more subject to conditions of illumination than to those of any other single factor, there is a maximum scope for experiment if behaviour in relation to light is chosen for study. This consideration is entirely independent of what has been said above with respect to the evident importance of light in nature. There is thus a twofold incentive for the study of behaviour in relation to light in marine organisms.

DIRECTION AND INTENSITY AS FACTORS IN RESPONSE TO LIGHT.

One of the most readily noticed characteristics of collections of small marine animals is the formation of groups heading towards (or away from) the light. In any glass container a concentration of animals will be found on that side which faces a window, or artificial light-source, as the case may be. This applies to a great range of forms from various phyla. At the same time a greater or lesser concentration, of the same or different species, may occur on the opposite side of the container, in the part furthest from the source. The former group consists of individuals which move more or less directly up to the bright region where they collect and which at this stage may be simply called "positive," the latter of individuals which keep away from the source and may be called "negative." This grouping in relation to simply-defined conditions of illumination provides a suitable starting-point for more detailed study of the influence of light on the behaviour of the animals concerned.

Observers of this photopositive and photonegative behaviour are generally soon led to enquire how far the animals are influenced by the directional properties of the light, and how far by successive changes of intensity experienced during the course of their movement. This opens up one side of an intricate problem which has assumed several shapes at one time or another, namely—to state it briefly, if crudely—the question of the relative importance of *direction* as opposed to *change of intensity*. It appears to be an appropriate enquiry in the present case, in view of the evident effects of diurnal changes in intensity on the distribution of the wild populations of various plankton organisms. Let us see, then, in what precise ways the problem is applicable to these animals in confined spaces. For simplicity we will restrict considerations to photo-positive behaviour, but they apply equally, *mutatis mutandis*, to photo-negative.

A. *As concerns the group.* The collection formed on the lighted side of the vessel may have formed because (*a*) it is nearest the light-source, or (*b*) it is in the brightest part of the vessel. It usually happens that movement towards the source is accompanied by increase in intensity, but conditions can be devised in which the two factors are dissociated. In the one case the group should form along the line of incidence of the light, in the other, in a region of maximum illumination irrespective of direction of incidence. Experiments bearing on this point are described below.

B. *As concerns the individual.* In so far as the group is homogeneous (and in this case it is so to be regarded), a complete interpretation of its behaviour will be given from the study of a typical individual composing it.

The varieties of individual behaviour that lead directly to the formation of groups in regions of some definite illumination are as follows.

(I) Activity may vary with light intensity, and so the animals may tend to concentrate in that intensity in which the movement is slowest. This is a purely *photokinetic* effect. Its success in bringing about formation of groups is not great unless very marked differences in activity are produced. Thus (for a negative case) *Gonionemus murbachi* collects in the shaded part of a tank, partly because of decrease in activity. (YERKES, 1903; MURBACH, 1909.)

(II) The direction of movement may still be random, with the exception that reversal reactions are given to abrupt changes of intensity. Thus it is well known that *Euglena viridis* collects in (not too strongly) lighted regions owing to avoiding reactions when entering a shadow (see JENNINGS, 1906). Similar behaviour is claimed for *Bacterium photometricum* and various Protista, and probably occurs more than is suspected among Metazoa such as Isopods.* For the appearance of this kind of group it is necessary that there should be an abrupt change from light to shade in the field of illumination.

(III) The animal may exhibit, to a greater or lesser degree, some form of *phototaxis*. That is to say, the light influences the *direction of movement*. So long as it is reactive, the animal, as it moves, is constantly making some sort of adjustment in relation to the light, so that the course it follows bears some definable relation to the conditions of illumination. Various forms of phototaxis have been distinguished. They have been classified by KUHN (1919) and reviewed by FRAENKEL (1931). In light of these publications, and of other contributions to the literature of subject, the varieties of phototactic behaviour that we must be prepared to find may be conveniently grouped as follows :—

(a) *The animal is capable of at least fairly accurate orientation, in a strict sense, in the direction of incidence of the light.* It is not necessary that the animal should be in some way capable of directly appreciating the direction of the light, as, for example, by adjusting the position of a certain transparent tissue to the direction of the light passing through it. Nor is it necessary that the light should directly alter the tonus of the muscles, thus forcing the organs into certain positions, so that the animal is as passive an agent as is a dead body in the way it acts in respect to gravity. It is, indeed, sufficient that the animal can somehow appreciate differences in intensity on the two sides of the body. By nervous response it tends to adjust its course so that bilateral photoreceptors receive equal illumination. One of the first detailed quantitative investigations on phototaxis, namely that of PATTEN (1914) on blowfly larvæ, demonstrates this method of orientation. The more clear-cut cases of *tropotaxis* are included in this category. They appear to be widespread, occurring in various kinds of animals. One might expect that animals with eyes sufficiently developed to discriminate some sort of visual field will be able to orientate more efficiently, displaying less searching movement, than, for example, a blowfly larva, which has no eyes, or a Calanoid Copepod, which has a single median eye.

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* Shock reactions on passage from shadow to light are recorded by Müller (1925) for negative Oniscus.

(b) *Orientation may be very inaccurate, and so the path followed irregular, but the animal still be capable of distinguishing differences in intensity on the two sides of the body.* The irregularity may be the result either of intermittent sensitivity, or due to the fact that the animal can only appreciate large differences in intensity.

(c) *The animal moves in a course directed in the path of the light, not in the above manner, but through response to changes in intensity as its photic-sensory area moves into the shadow of the body.* This type of movement was originally ascribed by JENNINGS to Protista, such as *Euglena viridis*. Though BANCROFT (1913) brings forward good evidence that Jennings' explanation is inadequate for that organism, a genuine case appears to be provided by tadpoles of the Ascidian Amaroucium studied by MAST (1921). In this case the response is not to differences between right and left sides, but to changes in illumination of the photic-sensory area as a whole.

(d) As in (c), the animal is only sensitive to changes in intensity on its sensitive surface as a whole. While it is incapable of any exact orientation, yet, because of the shading effect of the body, the mean direction of its course tends to be in the direction of the light-rays, rather than to the area of maximum illumination (if the latter is dissociated from the former).

(e) As in (d), *but the light receptors are such, or the behaviour so adapted, that the intensity changes appreciated by the animal approximate to those that "exist in the physical surroundings." A positive animal will therefore collect in the brightest region, and not at the point nearest the light-source, if these two are dissociated.* Though this behaviour undoubtedly takes place with respect to the chemical sense, viz. typical examples of "chemophobotaxis" (e.g. cheese-mite, HENSCHEL, 1929), it is very doubtful whether it is likely ever to occur with respect to light. At one time more than one investigator, using a graded filter, has claimed that certain Crustacea collect in the brightest area and not in the path of incidence of the light, but the experimental conditions seem in no case to exclude other explanations (see p. 424).

These five types may be grouped together in various ways to suit taste or convenience. Thus (a) and (b) are logically grouped apart from (c), (d), and (e), since in the former differences in illumination on the two sides of the body are detected, in the latter only differences in total illumination from moment to moment. This seems to be the most rational line of distinction between *topotaxis* and *phobotaxis*, though presumably Kuhn's classification would group (c) with (a) and (b) as contrasted with the two others. However, the point is of no consequence for our present purpose, though it serves to illustrate the chimæroid form of biological definitions, according as the emphasis falls on the logical or empirical implications. Or again, in (a) and (c) orientation is in a fairly accurately directed course along the path of incidence of the light ; in (b) and (d) the course is irregular about an axis coinciding approximately with the direction of incidence ; in (e) there is no connection between direction of movement and direction of light. A grouping of this sort is more appropriate when the cause of aggregations of the animals is the main point at issue.

During examination of the light responses of various plankton animals, an attempt has been made to relate the observed behaviour, by the aid of the above categories, to that of animals that have received more thorough attention, while at the same time to note how far the categories meet the requirements of the species investigated here. It has been considered useful to do this before attempting detailed analysis of the behaviour of any particular species.

Two terms are freely employed in this paper : "phototaxis," meaning that the direction of movement is in some way or another affected by light ; and "(photo)topotaxis," a special type of phototaxis in which the direction of movement is controlled by the direction of the light rays. The term "phototropism," formerly used, is avoided, as this has been restricted to the orientation of sessile animals.

METHODS AND MATERIAL.

In the usual circumstances, such as in the straightforward case of a light-source on a dark background, the light intensity increases in the direction of the source. The two factors are not separated. It is not difficult, however, to devise conditions in which one factor is eliminated, or set against the other. In the case of a parallel beam of light, if loss due to absorption be disregarded, the approach to the source is accompanied by no change of intensity ; in a convergent beam, the light intensity *diminishes* towards the source ; in a gradient of light given by a filter increase of intensity* can be opposed to direction ; the light source can be made to diminish as the animal moves towards it ; both direction and change of total intensity can be eliminated by opposed parallel beams ; while direction is eliminated but change of intensity maintained if a convergent is opposed to an exactly similar divergent beam. If persistently

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[*] It should be made clear that the conception of light intensity at a given place means the *sum total illumination falling from all directions*. The expression is so employed all along. It is referred to as "total intensity" when added emphasis is required.

photosensitive organisms, exhibiting some definite movement in relation to light, are subjected to such varied conditions, an analysis can be made of the light response in question. The external conditions essential for the response will be shown; in particular, it will be possible to estimate the relative importance of direction and change of intensity. Such, in its essence, is the method underlying the experiments of which account is given below.

The various light conditions that were reproduced may be summarised as follows.

(1) *Parallel beam.* This was procured by means of a wide convergent lens of 20 cm. focal length. Placed against a square glass dish of water, at a distance of 42 cm. from an electric bulb, this lens produced a beam which slightly converged from the parallel. The convergence may be regarded as adequate to counteract any loss of intensity due to absorption. The essential details are reproduced in Fig. 1.

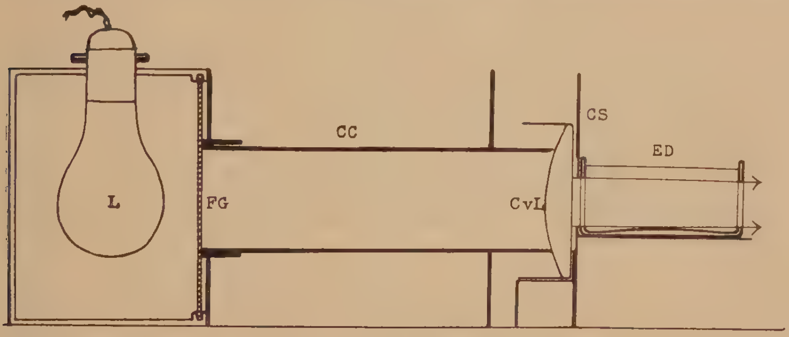

FIG. 1.—Apparatus for procuring parallel beam.

L, daylight bulb, 100 watt. FG, frosted glass screen. CC, cardboard cylinder. CvL, convergent lens. CS, cardboard screen. ED, experimental dish.

It was not found necessary to use a filter for infra-red rays, as over reasonably short periods there was no appreciable change of temperature, and no significant difference was observed in the behaviour of the animals even over long periods. The lens itself must have absorbed a large proportion of these rays. However, if lights were to be kept on for long periods, a battery-jar of water was placed between the light and the lens. The jars shown in Fig. 3 are for this purpose.

On occasions the screen of frosted glass placed close to the lamp was omitted from the apparatus.

(2) *Convergent beam.* Apart from preliminary experiments in which a cylindrical jar of water was used, a convergent beam was procured by substituting, in the above apparatus, a convergent lens of much greater refracting power (see Fig. 2a and b, and p. 400).

(3) *Convergent opposed by divergent beam.* The convergent beam was produced with the same lens as in (2), and passed through a dish 7 cm.

wide. A divergent beam was obtained from a second light-source on the opposite side of the dish, the correct amount of divergence being secured by means of cardboard screens suitably placed. The intensity of the second light was reduced by a sheet of ground glass (Fig. 3). An adjustable resistance was fitted to the lead of the first light-source, so that the intensities of the beams could, if required, be equalised. A grease-spot on a piece of white paper provided an adequate indicator for the latter purpose.

(4) *Light gradient.* Methods involving the use of a triangular glass dish filled with an absorbing liquid, or some kind of screen of graded absorbing capacity, have in the past been employed by investigators desirous of obtaining an intensity gradient antagonistic to the direction from which the light is coming. The apparatus employed in the experiments here described consisted of a triangular dish filled with an appropriate solution (Figs. 11, 12, and 13) placed horizontally between the light-source and a long glass dish containing the animals. The latter dish stood on a dark board marked in squares. A screen was fitted around the filter in such a way that no direct light reached the experimental dish from the light-source other than that which passed through it. Suitable precautions were taken to minimise light reflected from the sides of the dish. The triangular dish was filled with either ammonia copper sulphate solution or diluted Indian ink. The one gave a clear passage to the light, of which all that came through except at the extreme bright end was deep blue; the other caused differential scattering of the components of the radiation, so that the light that came through became increasingly red towards the dark end, until only the red outline of the filament showed. The concentration of the solution was so adjusted that an obvious gradient was shown on a plain white surface. In the case of the copper solution, the

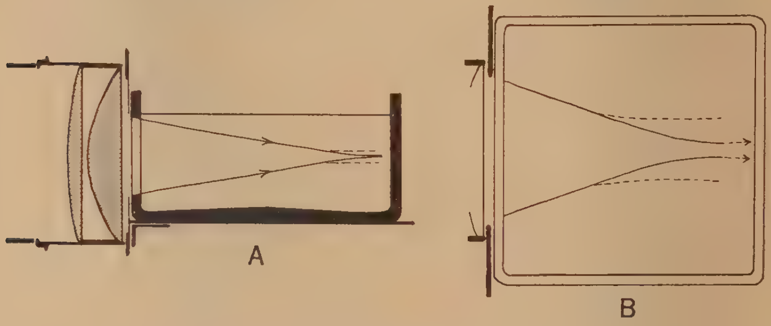

FIG. 2.—Apparatus for procuring convergent beam.
(*a*) side view of lens and dish.
(*b*) convergent beam from above.

actual concentration was measured. Methylene blue solution was also tried.

Various other lighting conditions were also set up at one time or another, some of which are referred to in this paper. For instance, two parallel beams, procured by a duplication of the apparatus in (1), have been opposed to one another, and the intensity of one, or both, varied by means of an adjustable resistance. Again, two such parallel beams have been placed at right angles to one another. Certain such modifications of the above four main varieties of apparatus employed are mentioned during the course of description of the experiments.

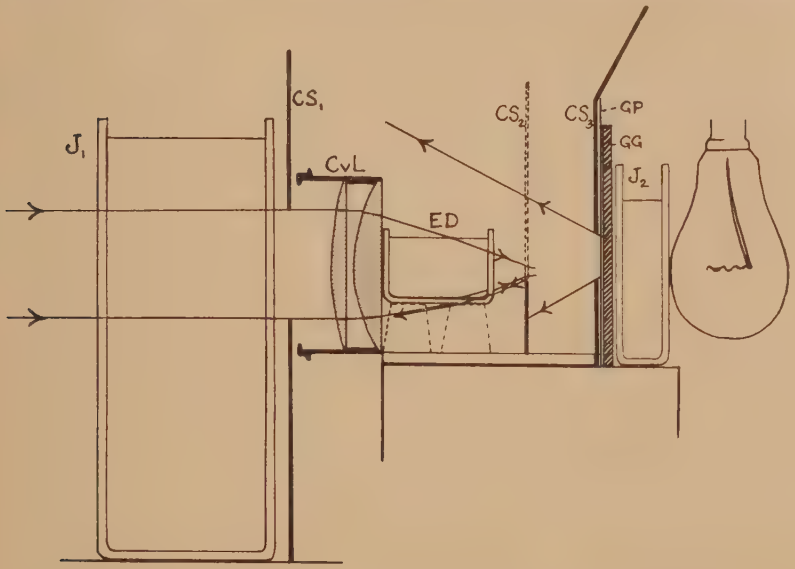

Fig. 3.—Apparatus in which a convergent is opposed by a divergent beam.
J, jars of water. CS, cardboard screens. CvL, convergent lens. ED, experimental dish. GP, sheet of grease-proof paper. GG, sheet of ground glass.

Notes on apparatus. The sources of light consisted of 100 Watt daylight electric bulbs, either Osram or Mazda, gas-filled.

Glass dishes. Rectangular, moulded, dishes of 15½ × 15½ × 7 cm. were most frequently in use. Selection was made of those in which the glass of the sides was most regular. The dish shown in Fig. 11, etc., was 47 × 12 × 7. Use was also made of a special cemented dish, 11 × 6 × 15½, in which the glass was perfectly free from blemishes.

Water. The water in the dishes was always pure "outside" sea-water, which had reached room temperature.

Scattered light. The experiments were carried out in darkened rooms in which extraneous sources of light were negligible, if not entirely absent. The sources of light in the experimental apparatus were always adequately screened. But more difficult to deal with is the light which diffuses from the beams themselves or which is reflected from the sides and corners of the dishes. Precautions to eliminate the effects of such light were taken where necessary, and as far as the experiments go, the results are not complicated by such effects. Perhaps, however, one exception to the latter statement is in respect to the light-gradient dish, where light reflected from the back side many to a certain extent assist scattered light in producing a deviation from the path of the direct light (see p. 414).

Preliminary experiments, and such in which apparatus 3 was concerned, were conducted during the spring of 1931 in a cellar. Here the temperature fluctuated little and remained conveniently cool. The room could be darkened completely. In the second part of 1932 the greater part of the work was conducted in another room which provided better facilities. It was darkened for the purpose. The temperature here varied from 22·5° C. in August to 14° C. in October, but was not subject to large diurnal changes.

The plankton animals investigated were taken from groups of healthy survivors in fresh tow-nettings from the English Channel off Plymouth Sound. They were transferred to dishes of clean sea-water and left for a time to become habituated to the new conditions. As a rule it was then merely a matter of selecting those specimens which were showing persistent aggregation towards, or away from, the lighted side of the dish, or showing any kind of response to light. Their behaviour in one or more of the experimental situations was then recorded, but only *in so far as the particular response remained.* Specimens which lost activity or became erratic in their behaviour were discarded. Since it was the primary aim to investigate the responses themselves, and not the extent to which any given animal would exhibit them, it was beside the point to consider how the experimental conditions compared with those in nature, or how fluctuations in light intensity or temperature might affect the appearance of a certain response. It was sufficient that the animal continued to show it.

All along care was taken to observe that the animals were consistently exhibiting the response under investigation. In general this presented no difficulty. One of the most likely changes that would have upset results would have been sudden changes from positive to negative behaviour, such as is readily induced in some species, e.g. *Temora longicornis.* But such behaviour was very infrequent, and quite obvious when it did occur. It may be noted that the light intensities in the dishes were always low, as compared with daylight, and well below the limit that might have induced species living in the upper levels of the water to revert from positive to negative. Again, there may be temporary or intermittent loss of sensitivity to light, so that movement becomes more or less random. But this did not occur under experimental conditions if it was not also observed in ordinary illumination.

The animals were handled as carefully as possible with a fairly wide-mouthed pipette, and the water in the dish to which they were introduced disturbed as little as possible during the procedure. They could be attracted to any required position in the dish with the help of a subsidiary light; so that, once they were in the experimental dish, no further handling as a rule was necessary.

When not crowded, most of the plankton which survive under these conditions generally remained healthy for two or three days, if not more. For the most part, however, those investigated had been captured the previous day.

The names of the species investigated are in all cases those adopted in the Plymouth Marine Fauna, Second Edition (1931).

In identification of specimens I am indebted to Dr. M. V. Lebour and Mr. D. P. Wilson for the help, on various occasions, of their special knowledge. It also gives me pleasure to record my obligations to Dr. E. J. Allen, Dr. W. R. G. Atkins, and Mr. F. S. Russell for helpful criticisms and suggestions.

BEHAVIOUR OF PHOTOPOSITIVE SPECIMENS.

I. In Divergent and Parallel Light.

In proceeding with the account of certain laboratory observations to be described, it is proposed to start with a survey of the various species of plankton animals which have been noticed during the course of the work to give positive movements to light. It was soon clear that animals forming positive groups are very largely, if not always, forms which exhibit some definite *phototactic* movement. At any rate, among the variety of forms studied, no cases were encountered in which grouping was effected by methods I and II (see p. 388). All light response with which we are here concerned falls under the broad category of phototaxis.

In the ensuing account of the characteristic behaviour of different species, it is implied that the direction of the light is horizontal.

Centropages typicus, a medium-sized species of Copepod, is often persistently attracted to the light. It shows two main types of movement: (*a*) regular steady swimming, keeping a straight course in the direction of the light; (*b*) rapid darts, which may be carried over a considerable distance, and in which the course is more or less zigzag. The straight, steady movement is typically interrupted by short pauses, which correspond to the sinking phase of the up-and-down movement observed when the light-source is from above. When orientated horizontally, the animal may have either dorsal or ventral surface uppermost. Indeed the latter position seems to be more frequent than the former. The habit of swimming indiscriminately front or back-side uppermost appears to be quite general among Copepods.

The two above-mentioned types of movement, rapid and slow steady, are to be seen in other species of Copepoda. *Temora longicornis* progresses either rapidly in a zigzag course, as though hurling itself to the light, as well as by slow, steady movement interrupted by pauses. *Paracalanus parvus* swims a straight steady course, with fewer checks than is usual in Centropages, or else, particularly in a beam of light, may move in quick jerks. *Calanus finmarchicus*, again, moves either slowly and steadily in a straight line for the source of light, or rapidly, by jerks, in a rather zigzag course.

Another Copepod, the abundant *Acartia clausi*, behaves in quite a distinctive manner. Its movement to the light, usually rapid, is accomplished by a series of jerks (between which there may be, if movement is slow, a considerable pause), the path followed being somewhat zigzag. The noteworthy feature is that no constant orientation of the body is maintained during this lightward movement. The animal perhaps most frequently assumes a more or less vertical position, the head uppermost, and the dorsal surface facing the light-source ; but during the course of movement no one position is kept for any length of time. The animal may come to face in almost any oblique direction : upwards, sideways, diagonally, or even downward. There is therefore no question here of the course of movement being dependent on the direction in which the body is orientated. And further, when the animal remains still there is no orientation ; it is only after movement has begun that a lightward direction can be detected.

Corycaeus anglicus, a small species with excessive development of the eye lenses, is spasmodically attracted to light. It moves with fair speed, somewhat jerkily but without pauses, characteristically keeping a straight course. This movement is more vigorous than the slow steady straight movement observed in other Calanoids, but in either case there is constant orientation of the body in the direction of the light rays.

Occasional positive specimens of *Anomalocera patersoni* have been observed. In this species locomotion is strikingly different from that in other Copepods investigated, being stronger and more deliberate—a difference that is no doubt associated with predatory habits.

Euterpina acutifrons, a Harpacticoid Copepod abundant in fine townettings from the Sound, moves by a rapid succession of short jerks. Though sometimes they keep in a straight path, their course is often erratic, deviating from one side to the other. However, on account of their activity, and because it has been possible to observe numbers at a time, they have given satisfactory results in certain experiments described later.

Males of the parasitic *Caligus rapax* are, as a rule, photopositive. When swimming with dorsal or ventral side uppermost they move in a straight line towards the source, the body orientated in the direction of the rays.

If, however, as often happens when the light is horizontal, they turn and swim on their side, the direction of movement is *at an angle* to the path of the light, the dorsal side facing the source. At intervals the animal turns over, "tacking" in the opposite direction. As a result, the course followed is zigzag and leads the animals towards the light-source (Fig. 5). In a parallel beam the angle is approximately 45°, the turns being thus made through a right-angle. This instance is evidently to be classed among those light reactions to which the term *menotaxis* has been applied. It is the only example that has come under notice.

The nauplii of *Balanus balanoides* progress with the jerky motion characteristic of Crustacean nauplii. The lightwards path is more or less straight, but if a specimen is watched closely a good deal of deviation from side to side may be seen. On account of the persistency of the photopositive movement, these animals provide favourable material for laboratory experiments. The same persistent photopositive tendency was found in the newly hatched nauplii of the freshwater *Cheirocephalus diaphanus*. A specimen of an unidentified Cirripede metanauplius moved towards a light-source in a straight path.

Among the immature stages of Decapod Crustacea, the planktonic forms seem as a rule to be strongly reactive to light. Mention may first be made of the larvæ (first and second stages) of *Galathea squamifera* and *dispersa*. These were found to move straight to the light with their *posterior end foremost*. In the best performers the body is held accurately orientated, the path taken direct, and the movement continuous. Either ventral or dorsal side may be uppermost.

As in the case of other species capable of accurate orientation, the paths may often undulate considerably—even in a specimen which has only just previously moved in a straight path.

The first larvæ of Upogebia sp. (probably *stellata*) also orientate and move backwards, and are also capable of swimming in a straight path up a beam, but were found to be more erratic than Galathea. This curious habit of swimming backwards was pointed out by LYON (1906), who found that Palæmonetes larvæ move to light in this way.

The first Zoeas of *Carcinus maenas* have been found to be strongly photopositive, moving up a beam in a steady, and remarkably straight, course. They orientate in a normal manner, anterior end facing the light and dorsal surface uppermost. The elongate 1st Zoeas of Porcellana sp. (probably *platycheles*) also react persistently, moving straight forward towards a light-source or up a parallel beam. Owing to their long anterior spine it is easy to observe the exact direction of orientation in these larvæ, and it seems typical for them continuously to sway from side to side as they travel along. But this swaying is through a small angle only, and the mean direction of movement is in a straight line to the light source.

Specimens were sometimes seen to move backwards, but in this were not in the least handicapped in maintaining a direct path. The abdomen was moved rapidly, and the body swayed from side to side a great deal, but the speed was much the same as in direct forward movement. One specimen, perhaps with a limb hampered in some way, rolled over continuously to the left, and thus progressed in a spiral. And yet it kept a straight course up the beam.

Various other Zoea larvæ of crabs have shown photopositive behaviour, several moving in a straight line towards the source. Some of these swim backwards, the long posterior spine pointing ahead.

In addition, a specimen of a *Pandalus montagui* larva, which, though not altogether healthy, deserves mention as it remained persistently positive when tested in a parallel beam, went straight to the source with very little tendency to deviate, although—and this is the point emphasised—orientating at various oblique angles.

The larvæ of the herring (*Clupea harengus*), during the first fortnight of life, show marked tendency to cluster on the lighted side of their tank. Their responsiveness to light appears to be strongest when their activity is greatest. In lowest intensities, not only is there a falling off in activity, but, curiously, a reversal to negative phototaxis. Examination of the movement of individuals in relation to a single light-source, or in a parallel beam, was handicapped by the fact that the intensity was clearly too low. Though all active specimens before long moved up toward the light-source, they did not steer a straight course towards it and deviated considerably from side to side. After having been kept in the dark for three days their progress up a beam was more definite, but still there was a good deal of random movement.

The young larvæ of a species of goby (Gobiidæ) showed more definite phototactic movement. When active, specimens frequently swam towards the light up a parallel beam, moving in a characteristic way. They progressed by a series of jerks, the direction of each jerk (corresponding to one flick of the tail ?) being different from the one before, alternating to right and left so that the path was decidedly zigzag. The mean direction of the path was, however, straight and coincided with the direction of the incident light (Fig. 8).

Small Polychæt larvæ provide further examples of forms which can be strongly photopositive. They move continuously and directly towards the source, the course taken varying from a straight line to one which undulates regularly. An undulating course is characteristic of a species of Polydora, in which the body is constantly swayed from side to side, so that the head is all the time moving to and fro through a wide arc. A similar type of movement is seen in small free-swimming Turbellarians, single specimens of which have from time to time been under observation, In these the path followed deviates irregularly, but an average direction in the axis of the light is maintained. The anterior end of the body is constantly swayed from side to side, suggesting trial and error behaviour. Strong photopositive movement has also been observed in an Autolytid bud carrying eggs, and a Polychæt metatrochophore. In the latter specimen the anterior end moved through a very wide spiral. An unusual example is provided by the Disomid, *Poecilochaetus serpens*, a young specimen of which was found to be decidedly positive to light and to exhibit quite a unique type of topotaxis. It proved capable of moving straight up a parallel beam, although swimming so vigorously that its movement can only be described by saying the worm threw itself into convulsions.

It was placed by pipette at the far end of the beam. At first it lay extended on the bottom ; then rhythmic body movements began, which gradually increased in intensity until the worm was, so to speak, coiling on itself. Rising in the water, it swam straight up the beam, coiling vigorously. This procedure was repeated five times with an exactly similar result. Thus, in this example, the path of the animal is direct, whereas no part of the body is orientated to the light. The means whereby the direction of the path is maintained is quite obscure.

For completeness it may be added that further instances of observed photopositive movement are provided by Oithona sp. (Copepoda), *Sagitta elegans*, Mollusca larvæ, and Annelid trochophores. By this time sufficient has been said to show that indisputable phototactic behaviour can be evoked in a wide selection of smaller planktonic animals. This fact remains whatever the extent and significance of such behaviour under natural conditions.

The majority of the above species have been tested in a parallel beam of light (apparatus as in Fig. 1), and in no case was any difference in behaviour observed from that in ordinary divergent light. Since it has been found convenient to use a parallel beam in examination of methods of movement, the data from such tests have been freely included in the above account. Positive movement in a parallel beam has previously been found by ROSE (1925) for Balanus nauplii, etc., and by FRIEDRICH (1931) for *Calanus helgolandicus* and *Corycaeus anglicus*.

In reviewing the above account, attention may be drawn to the variety there is to be found in the movements of different positive phototactic forms. Some, such as most Copepods when moving slowly, and Decapod larvæ, are constantly orientated towards the source ; others are not orientated to the source although the path followed may be quite straight (*Acartia clausi*, *Poecilochaetus serpens*). Some keep the body rigid (Crustacea), others sway the anterior end from side to side (Turbellaria) ; some move jerkily (Euterpina, various nauplii), others smoothly and continuously (Decapod larvæ, Polychæt larvæ). The course followed may be straight (Decapod larvæ, some Polychæt larvæ), zigzag (some Copepods, Sagitta, Gobiid larva), undulating (Polydora sp.), or spiral (Trochophore) ;

varying regularly (Polychæt larvæ) or irregularly (Euterpina). Several Crustacea swim with either ventral or dorsal side uppermost. It is further to be noted that movement may be to the side (Acartia), or backward (prawn larvæ, Zoeas), or obliquely (specimen of Pandalus larva), and yet a straight course be maintained.

II. In Convergent Light.

It has been noted above that photopositive plankton animals will readily move up a parallel beam of light, although in doing so they are not continually passing into light of increasing intensity. Throughout they are subjected to constant illumination. One may next enquire what happens when the beam of light is made to converge, so that movement towards the source necessitates passing from higher to lower light intensities. Accordingly examination was made of the animals' behaviour in a convergent beam.

In the apparatus employed (Fig. 2) a convergent beam passing through a rectangular opening of 8·8 cm. × 4·5 cm., shrank from 7·8 × 4·2 (dimensions on entering the water in dish) to 1·2 × 0·8 cm. in a distance of 10 cm. When allowance is made for loss of light due to scattering, etc., the increase in intensity over this region was calculated as approximately 25 times.

The results obtained for various species tested are given below. In all cases care was taken that the specimens chosen were reacting positively to ordinary light.

Centropages typicus. On several occasions positive specimens were placed in a convergent beam, always with the same result. Provided they did not stay motionless, they moved up the beam towards the source, and showed no tendency to stay in the brightest region. In short, they reacted just in the same way as to divergent or parallel light, thus showing the importance of the direction of incidence as against change of intensity. Notes on the behaviour of 24 adult specimens are shown in Table I. Moreover, their average courses followed the paths of the light-rays; that is to say, starting in the brightest region the paths taken spread out in a fan coinciding with the direction of the converging light. In nearly all cases the animal kept at the edge of the beam, either at the side, or above, or on top. When left undisturbed, the animals congregated against the area of entry of the light (PQ, Fig. 4), where again they exhibited a tendency to collect at the edges. Movement was either very slow, steady, and straight; or more rapid, steady, continuous; or in rapid jerks.

Specimens placed carefully by pipette in one of the far corners of the dish (19-viii-32) behaved as expected if supposed to follow the course of the light-rays or the maximum diffuse light. The tracks of nine individuals are shown in Fig. 7.

TABLE I.

Centropages typicus.

Notes on movement up a *convergent beam* of 24 adult specimens (including 10 ♂♂ and 14 ♀♀).

The apparatus is that described on p. 391. (For the first 12 specimens the opaque glass filter was present, for the rest it was absent; but this does not affect results.) Specimens were placed singly by pipette in the narrowest part of the beam. Unless stated to the contrary, all were photopositive, moving up to the light source. The point at which movement started is recorded: l.p.—on leaving pipette, e.b.—on entering beam, t.b.—on touching bottom.

Specimen.	Started to move.	Movement.	Position of path.
(with opaque glass filter)			
1.		slow, with some hesitation	side edge of beam.
2.	t.b.	continuous slow steady	lower edge, in centre.
3.	l.p.	paused, then continuous slow steady	side edge.
4.	l.p.	,, ,, ,, ,,	side edge.
5.	l.p.	swooping movement, then slow	inside beam.
6.	l.p.	slow steady	side edge.
7.	l.p.	slow steady	centre, top edge.
8.	l.p.	slow steady	centre, top edge.
9.	l.p.	slow steady	centre, top edge.
10.	l.p.	slow steady	centre, lower edge.
11.	l.p.	slow steady	centre, top edge
12.	t.b.	movement at first irregular started on bottom, swam up and across beam, then hesitated; then swam slowly and steadily to light	side edge.
(without opaque glass filter)			
13.	l.p.	rapid, then slow	centre, top edge.
14.	l.p.	slow steady	centre, top edge.
15.	t.b.	slow steady	lower edge.
16.	l.p.	swoop, then slow steady	side edge.
17.	l.p.	2 or 3 rapid darts, then zigzag, then slow up side edge, gradually carried away from beam; checked, recovered, swam along edge of beam to source	
18.	l.p. swerved at start	slow steady	top edge.
19.	l.p.	slow steady	top edge.
20.	l.p.	slow steady	top edge.
21.	l.p.	(paused, fell through beam, only giving very slight jerks on coming in contact with the beam. Fell to bottom, from which it moved a little later)	
22.	e.b.	(started positive on side of beam, but tended to move in a circle, and was carried into darker part of dish)	
23.	l.p.	rapid	centre, top edge.
24.	l.p.	slow steady	centre, top edge.

When the convergent beam was reflected back on itself by a mirror, so that the directive quality of the light must have been counteracted to a large extent, it was found that the Centropages still swam towards the main source. Evidently the intensity of the direct beam exceeded that of the reflected light enough for the excess to be detectable by the animals. This affords an example of an effect which was observed on several occasions—when light is coming from various directions, the animal moves in the direction from which the light is relatively strongest.

Acartia clausi. In this species again no difference of behaviour was detected in divergent and convergent light. In the latter case animals moved towards the light as readily as in the former. Specimens were tested on several occasions, embracing both adults and immature, winter broods, spring broods, and late summer broods. Both slow and rapid movement were observed, as well as the characteristic lack of orientation. When collected at the light-source they showed a marked tendency to select the outer edges of the beam (as in the case of Balanus larvæ, Fig. 9).

Temora longicornis. Positive specimens of this species, again, were found to move up a convergent beam. Several tested (15-vii-32) moved for the most part with rapidity in a zigzag course (though slow, steady movement was also observed) ; and showed decided tendency to keep to the outer part of the beam, both during movement and when left to congregate.

On another occasion (21-v-31) several specimens had been tested alternately in convergent and divergent light of equal intensities in the apparatus figured on page 393. Each specimen was kept on the move for some while by the switching over from one light to the other. On the whole the animals moved distinctly faster up the divergent than up the convergent beam, as indicated below.

		Divergent.	Convergent.
Specimen	1.	Rapid, rather zigzag.	Slow steady.
,,	2.	Rapid.	Partly slow, partly rapid.
,,	3.	Very rapid.	Rapid.
,,	4.	Rapid, with slight exception.	Slow, interspersed with rapid.
,,	5.	Rapid and slow.	Relatively slower.
,,	6.	Rapid.	Slow, except at end of path.
,,	7.	Partly rapid, partly slow.	Less rapid, more slow.

It is not known, however, if any significance is to be attached to this difference. Movement up the convergent beam was, as usual, in the direction of the light-rays, i.e. the paths radiated outwards from the narrow end of the beam.

Euterpina acutifrons. Specimens which moved in a direct line for the light likewise moved directly up a convergent beam. The immature and nauplii also moved up the beam as readily as to an ordinary source.

Calanus finmarchicus. Positive specimens were found to swim to the

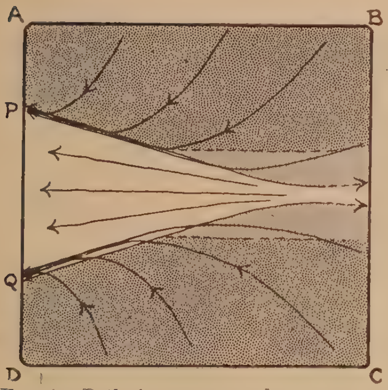

FIG. 4.—Paths in convergent beam—mean direction of those animals which move in the direction of the rays.

ABCD, square dish. PQ, entrance of convergent beam.

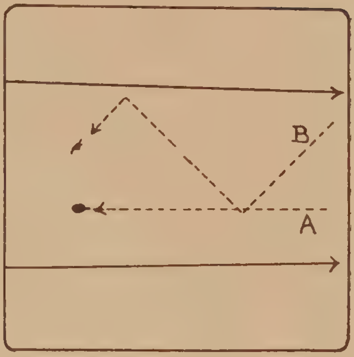

FIG. 5.—*Caligus rapax* ♂—paths in lateral parallel beam.

A, dorsal or central surface uppermost.
B, one of the sides uppermost.

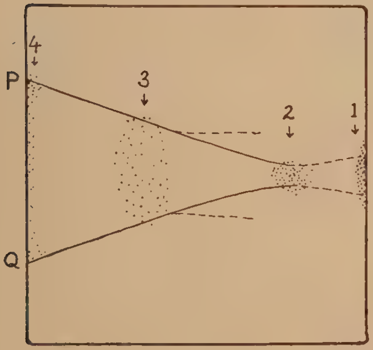

FIG. 6.—*Balanus balanoides* day-old nauplii —four successive positions (1 to 4) in movement up a convergent beam. PQ, entrance of beam.

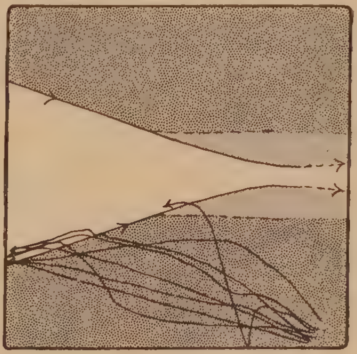

FIG. 7.—*Centropages typicus*—paths of 8 specimens in diffuse light coming from convergent beam.

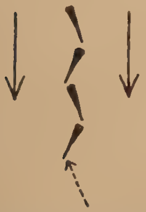

FIG. 8.—Path of Gobiid larva, showing successive positions of the body.

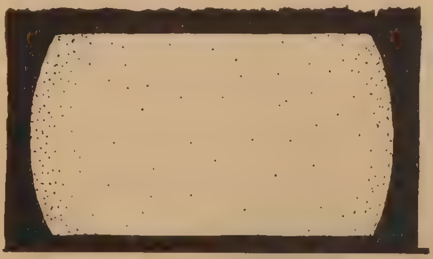

FIG. 9.—*Balanus balanoides* day-old nauplii—congregation at entrance of convergent beam.

light by steady continuous motion, following the direction of the rays. The tracks in the beam approached the ideal shown in Fig. 4. It may be added that positive specimens have also been found to continue lightward movement when the source was steadily dimmed during the time they were travelling towards it.

Balanus balanoides nauplii. A group of day-old larvæ, strongly positive, gave very clear results in a convergent beam (27-vii-32). They moved up the beam towards the light, the group spreading out in the beam, but not passing outside it. (The region outside the beam could be explored by the light reflected from a mirror.) Four successive positions of the main body are shown in Fig. 6. Within 2½ minutes from the switching on of the light they had moved from position (I) and congregated against the glass at the entrance of the beam. When collected in this way they tended to accumulate at the edges of the lighted area (Fig. 9), an effect which has been observed in various other species. When the beam is reflected back by a mirror, the larvæ still move towards the direct source, though considerably more slowly and in a more irregular course.

Zoea larvæ. Zoea larvæ that have been tested in a convergent beam have been found to move as straight and quickly towards the light as to an ordinary source. As in other forms, they follow the direction of the rays. Their paths conform closely with the idealised paths shown in Fig. 4.

Other positive animals which definitely swam towards the source in a convergent beam, thus behaving in a manner comparable with the species described above, include the following :—

CRUSTACEA	*Corycaeus anglicus*
	Paracalanus parvus
	Oithona sp.
	Caligus rapax ♂
	Nauplius of *Cheirocephalus diaphanus* (freshwater)
	Podon intermedius
CHÆTOGNATHA	Sagitta sp.
ANNELIDA	small Spionid larvae
	Polychæt metatrochophore
	,, trochosphere
PLATYHELMIA	small Turbellarian

To these may be added the following :—

An elongate Copepod nauplius, whose forward movement was regularly interspersed with pauses, remained positive in a convergent beam, the pauses being distinctly longer and more frequent.

An unidentified Decapod larva moved straight backwards up the beam in the same way as it moved to other light sources.

Very small cercaria larvæ from *Littorina littorea** were found to collect gradually towards the light. When a convergent beam was thrown through the beaker containing them, the larvæ gradually collected as before. For considerable periods the larvæ were seen to hang motionless in the water, but every now and then a sudden dart for a short distance was made in the direction from which the light was coming.

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* I have to thank Miss M. Rothschild for these specimens.

Among the various animals tested all gave comparable results, namely positive specimens move up a convergent beam as to any other source of light. There was not a single exception found. This uniform result is all the more striking, as a variety of types were investigated, representing several phyla, and exhibiting a variety of modes of progress (see p. 399).

There were no discrepancies from the general rule that, in so far as the animal normally moves straight in the direction of the light, so, in the convergent beam, its possible paths follow the fan-shaped arrangement of the conventionalised light-rays (as shown in Fig. 4). There was also shown a decided tendency to keep to the outer side of the beam rather than in the centre, and for collections to concentrate most on the outer edges of the beam at its point of entry ; probably to be explained on the grounds that the light was somewhat more concentrated at the edge of the beam.

The results, therefore, emphasise the primary importance of directional properties of the light in photopositive movement of the type considered. Not only is the increase of intensity which usually happens to be associated with the approach to a light-source unessential, but an appreciable *decrease* (such as produced by a convergent beam) does not affect the result.

III. In Convergent opposed by Divergent Light.

With a parallel beam of light, change of intensity in the physical environment is eliminated while direction is maintained. Direction, too, may be eliminated by opposing two beams of exactly equal strength. If it is required to preserve the change of intensity, it is only necessary that one of the beams should be convergent and the other divergent. Thus a convergent beam exactly opposed by a divergent of corresponding intensity gives a condition in which intensity change is preserved but direction, in one plane, eliminated.

As figured on p. 393 (Fig. 3), a convergent beam, produced as before, was passed through a dish 7 cm. across, and a direct light-source was opposed to it, screened with opaque glass and cardboard slits in such a way that a divergent beam was produced coinciding in position with the convergent. An adjustable resistance (a pair of triangular copper plates which could be moved up and down in a battery-jar of water) was connected with the second light, so that the intensity of the divergent beam could be adjusted to that of the other. A grease-spot, made by a small drop of medicinal paraffin on white paper, provided an effective indicator.

The animals investigated were placed in the glass dish and their positive behaviour checked by switching on one or other of the lights. Throughout the course of the experiment it was possible to check the persistence of this behaviour in the same way. It has to be acknowledged that the double-sourced beam was of twice the intensity of one light alone, but the behaviour with which we are here concerned was clearly not influenced on this account. Doubling the intensity of a single light-source was found, on occasions when tested, in no way to desensitise or otherwise to alter the general phototropic movement of the animal.

Acartia clausi. Tested on several occasions, this strongly photo-positive species was found to lose orientation altogether in the double-sourced beam. The movement of individuals appeared to be quite random, the jerks being made in any direction. When several were left in the beam, they distributed themselves at random through it.

Euterpina acutifrons is also quite disorientated. Specimens were observed to move to and fro in various directions as well as round in circles. As soon, however, as one light was dimmed (an opaque glass filter being interposed), a drifting away from the dimmed source was at once apparent, divergent and convergent source being treated alike.

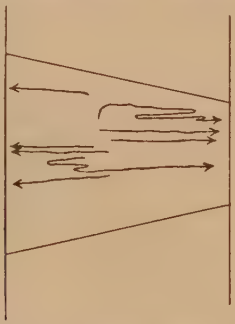

FIG. 10.—*Corycaeus anglicus* ♀—paths in convergent opposed by divergent beam.

Contrasting strongly with the above two species, *Corycaeus anglicus* keeps strictly orientated to one or other of the two light-sources. Positive (or, for that matter, negative) specimens move to and fro in the beam, always in the axis of the light. Fig. 10 is typical of results obtained. This shows the paths taken by a ♀ which was placed by pipette 8 times in the centre of the beam. It travelled straight towards one or other of the lights, and on occasions when it changed direction a complete turn through 180° was made. As far as tests with this species went, no preference for one or other of the lights was noticeable.

Centropages typicus, again, retains orientation along the path of the light rays, moving without preference to either source. The characteristic behaviour of actively positive specimens is movement from one side to the other along the length of the beam with longer or shorter intervals spent at either source. As a typical illustration may be cited the behaviour of an active ♀ (20-1-31) on being placed in the centre of the beam 35 times in succession.

	No. of trials	to convergent source.	to divergent source.
(1) Both lights on . . .	8	4	4
(2) Divergent only . . .	8	0	8
(3) Convergent only . . .	8	8	0
(4) Both lights on . . .	11	8	3

On arriving at the side of the dish it either remained for some time at the light or else soon turned and swam to the opposite source.

Precisely the same sort of behaviour was found with specimens placed in opposed parallel beams they oriented to one source or the other. With a parallel beam reflected on itself, either the direct source or the reflection can act as a source of attraction.

Temora longicornis, as Centropages, orientates its course in a very noticeable manner to one or other of the sources. Individuals were observed to move to and fro in the beam from one source to the other.

A particularly clear-cut instance is that of a specimen which, after being placed in the beam and left undisturbed, swam alternately from one end of the beam to the other. Watched for 2 or 3 minutes, it was seen to move to one source, swim against the glass for a little, then turn and swim straight to the opposite source. During this whole period it made no fewer than 18 journeys, 9 times to each source. Then, for a period of half a minute, the single lights were tried in turn, and the positive behaviour of the animal verified. After this, both lights were again switched on together, and for another two minutes the to-and-fro course was continued. Again, in the same way, 18 journeys were made.

Zoea larvæ of an unidentified species were tested on one occasion. A number of specimens were watched, and the characteristic behaviour found to be as follows. To either divergent or convergent source alone they move fairly straight and quickly ; when both lights are on they are to a large extent disoriented : they move in various directions, but apparently oftener up and down the beam than across. Thus, because their movements are not altogether random, but more frequently towards one or other of the sources, they are intermediate between Centropages and Acartia.

Some of the smaller planktonic forms appeared, like Acartia, to be disoriented in the double-sourced beam. Among these are : Balanus nauplii, *Paracalanus parvus*, and Oithona sp. It may be added that *Podon intermedius* and larvæ of Polydora sp. lost orientation in a double-sourced parallel beam, moving in circles.

No other species were investigated, and no further examples can be given of behaviour like that shown by Corycaeus, Centropages, and Temora. It is probable, however, that prawn larvæ of various kinds would be found to act in the same way. A specimen of the larva of

Pandalus montagui was found to steer straight to one or other end of a double-sourced parallel beam.

There was no tendency found, among species investigated, to collect in the brighter part of the beam (divergent source), but it cannot be claimed that the experiments were sufficient to exclude absolutely the possibility of this occurring. At any rate, it is certain that this does not happen in the case of *Acartia clausi*, specimens of which species distribute themselves at random through the beam. With Acartia, then, we have definite evidence from this source that photopositive movement depends on the directional properties of the light, and not on the change of intensity encountered in passage through the beam. Again, with species which maintained orientation and moved to one source or the other, on no occasion was there any indication of preference for either one of the lights.

These experiments go far enough to bring out two points. In the first place, there is the fact that, in a double-sourced beam, two quite distinct types of behaviour occur. Some species, on the one hand, lose orientation and move about in any direction ; some, on the other hand, still orientate to either source. It may be supposed that this difference between these two groups of species results from differences in the light receptors. If the latter structure is affected by the light from all directions more or less equally, then light from two opposed directions may be expected to upset orientation. If, however, the receptor is affected, say, from one direction only, so that when facing that quarter it is screened from the light behind, then orientation to each source in turn is possible. It can be understood that, among various forms of lower animals, some might be affected by light coming from almost any direction, while others might show decided differential selection, being, for example, more receptive to light coming from in front than from the sides, and from the sides more than from behind. Among the former might be included the more transparent and the smaller forms with a single median eye ; among the latter, forms with larger paired eyes with a definitely restricted field of view, forms with a single median eye whose field is reduced by the opacity of the body, or owing to the presence of pigment, forms with well-developed lenses which concentrate light from one direction at the expense of others, or with any other characteristic which may induce inequality in the optical field. This supposition receives support from results given by the species which have been investigated. Those that are disoriented include (i) small transparent forms with a single median eye, such as Balanus nauplii, Euterpina, and *Paracalanus parvus*, and (ii) the larger, but transparent, *Acartia clausi*, which, as noted above, does not maintain orientation in any fixed direction when on the move, and so would come under the influence of both lights equally. Those that still orientate themselves are species which happen both normally to move straight in the axis of the beam, following the path of the rays, their body orientated towards the light-source, and, at the same time, to give reason to suppose that their eye is wholly or partly screened from the light falling posteriorly. *Temora longicornis*, though rather small, is pigmented; Centropages is by no means transparent and of considerable size; while Corycæus possesses a pair of prominent lenses which concentrate the light from one direction at a time.

The second point to be brought out is that those species which move to and fro to one or other of the sources are evidently still sensitive to the *direction* of the light. They will continue, moreover, swimming up a convergent beam even though there is divergent light from the opposite direction.

IV. In a Light Gradient crossing the Path of the Light.

By means of the apparatus described above (p. 392) it is possible to produce a gradation of intensity from one end to the other of an elongated glass dish or glass tube, in such a way that the brightest end is furthest from the light-source, and the passage in the direction of the light involves passing into decreasing intensity. Two phases can be observed in the behaviour of the animals studied: (i) the direction of their path across the dish, (ii) the area in which they congregate when left undisturbed for an adequate period.

(i) When an animal is introduced somewhere along the length of the side away from the light-source, it first crosses the dish, until in contact with the glass of the side facing the source. The course followed may be compared with the known direction of the light and any possible effect of intensity difference noted.

(ii) Assuming that it remains active after coming in contact with the side of the glass facing the light-source, the animal will continuously swim against the glass in the effort of continuing lightward movement. In the ordinary way, that is, if there is no light filter, the result of its movements will be to bring it gradually to the region immediately opposite the light-source, where random variations in direction will be made equally to the right or the left. The animal will, in effect, work its way along the edge of the glass by degrees, until in the region nearest the light-source. A group of animals left to themselves will gradually collect and concentrate in this region. Now, in the ordinary way, the animal is all the time moving into increasing light intensity; whereas when a graded filter is used, the intensity *decreases* as the region opposite the source is approached. Where, it may be asked, will the animals collect in the latter case? If the region of highest intensity is chosen, they will collect at the end of the dish *furthest* from the source ; if influenced by the direction of the light alone, they will collect *opposite* the source.

Centropages typicus. The first trials were made with comparatively highly diluted Indian ink in the filter. The apparatus is shown in Fig. 11. Individual animals were placed by pipette in the region of the dish furthest from the source and their subsequent movement noted. The paths of the 25 specimens tested are shown in Figs. 14A and B. It will be seen that the paths coincide closely with the direction of the light-rays. No marked deviation towards the brighter region (i.e. in the direction of Z) can be detected. Furthermore, the animals did not take long to work

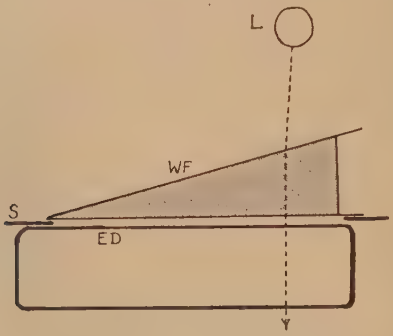

FIG. 11.—Light gradient apparatus.
L, daylight bulb, 100 watt. WF, filter.
S, screen. ED, experimental dish.

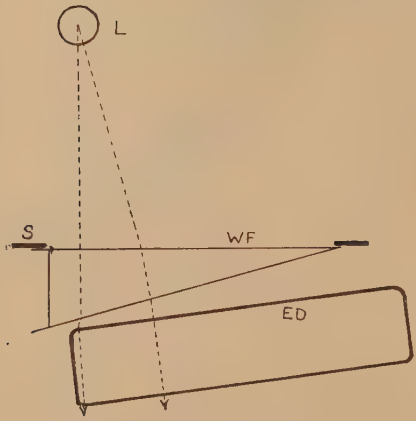

FIG. 12.—Light gradient apparatus. Lettering as in Fig. 11.

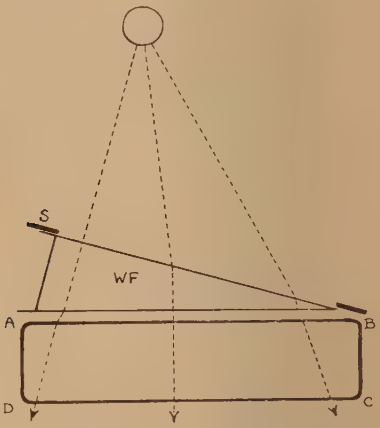

FIG. 13.—Light gradient apparatus. Lettering as in Fig. 11. Corners of experimental dish marked ABCD.

up the dish to the region opposite the light, where they then collected. This behaviour—moving in path of the light-rays and collecting at the point nearest the source—is what is to be expected of animals whose photopositive movement is regulated by the direction of the light rather than by change of intensity.

When, however, the strength of the Indian ink solution was increased, so that a more pronounced gradient was procured, and very little light penetrated direct into the darker end, the paths of specimens tested (this time liberated in middle region of the dish) showed a noticeable deviation to the left, that is, towards the brighter part of the gradient.

This deviation was then demonstrated more accurately. The same solution of ink was used, and the apparatus arranged as in Fig. 13. Twenty-five specimens were released immediately opposite the point of direct incidence of the light. Note was taken of the point at which they arrived at the opposite side.

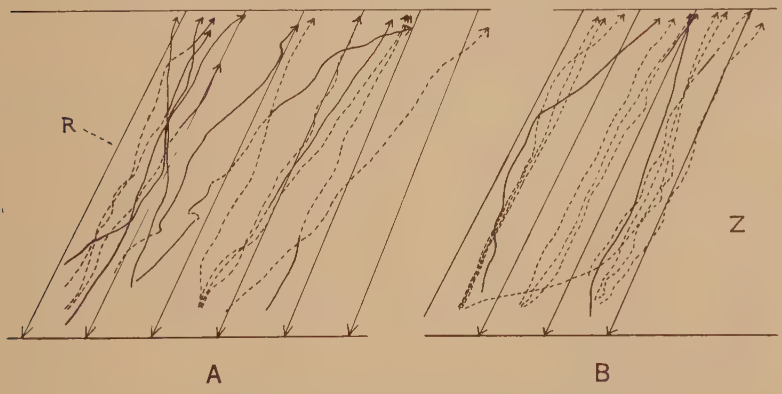

Fig. 14, A and B. *Centropages typicus*—paths in light gradient.
R, arrows indicating direction of the light.
Z, direction of brighter end of gradient.

The distance of the direct path was 11 cm. A dark board underneath the dish was marked in 2-cm. squares, the scale being expressed in cm., 0 to 46. In this case the point opposite the source, where the light fell at right angles to the dish, was at 25. The points of arrival were grouped in 2 cm. lengths.

It became clear that the animals deviate slightly towards the brighter end of the dish (i.e. in this case to the right), as the results given in Table II show. There was, in fact, an average deviation of 1·2 cm. to the right over the direct course of 11 cm. The next day the experiment was repeated, the same batch of animals being used, with similar results, shown in the same table. No record of the actual tracks was kept, but it was most noticeable that such deviation as was apparent occurred mainly in the last

4 or 5 cm. of the path. An estimated mean path is shown in Fig. 16. That a deviation should be found is not surprising ; the cause of it is discussed below. In the majority of animals the movement was slow, and at the same time jerky.

TABLE II.

Paths of *Centropages typicus* across Light Gradient.

Animals released at **25**.

Point of arrival along AB	20–22	22–24	**24–26**	26–28	28–30	Average deviation.
Number of specimens						
12–x–32	0	3	7	12	3	1·2 to Right (25 to 26·2)
13–x–32	0	1	**10**	11	3	1·3 to Right (25 to 26·3)

Note.—In each series the same animal may have been used on more than one occasion. Very few gave no results, i.e. remain inactive.

When some Centropages were left in the dish, they did not concentrate exactly opposite the light-source (at **25**), but kept distinctly to the right. This behaviour was also shown, and more obviously, by a number of Acartia in the dish at the same time.

It is not difficult to account for the occurrence of this deviation from the path of the direct light ; for it is clear that, if body-orientation in some way depends on a balance of the light falling on the two sides of the animal's body, excess of diffuse light on one side will cause a deviation of orientation in that direction. In the darker part of the dish the amount of diffuse light coming from the brighter end must have a strength of an order comparable with that of the direct light, and so introduce an appreciable lateral component into the light effective in regulating the animal's course. The excess of diffuse light on one side will also influence the position round which the animals tend to congregate—for at the point nearest the source random movement will now tend towards the brighter side rather than the other. This question is fully treated later, after some experiments with Euterpina have been described.

Euterpina acutifrons. In a preliminary test, with the filter arranged as in Fig. 11, and containing methylene blue solution, it was noted that immature animals moved obliquely across the dish more or less in the direction of the rays and steadily accumulated at the dimmer end of the dish round a point almost opposite the light source. As in Centropages, the brighter end was ignored.

With diluted Indian ink in the filter, it was observed that now, on the whole, the paths of adults and immatures, moving across the dish at the brighter end, noticeably deviated to the left. Then, when left to congregate, the animals were found concentrated in an area opposite the light-source—or somewhere to the left of it.

When the filter, filled with half-strength ammonia copper sulphate solution, was arranged as in Fig. 18 (except that the dish was placed parallel with the lighted side of the filter, so that the point nearest the source was at the extreme left end), adults, immatures, and nauplii aggregated quite rapidly to the left side of the dish opposite the source of light. The paths of individuals, judging from the way a group expanded from the point at which introduced, on the average appeared to approximate well with the path of the light rays. The behaviour was no different when a length of opaque glass was stood between the filter and the dish. The animals even continued to congregate at the left-hand end (1 to 18) when the opaque glass was stood obliquely, as shown in Fig. 17, in a way which greatly accentuated the gradient. Further, when the apparatus was arranged as in Fig. 13, the animals congregated in the neighbourhood of 25; and again when it was arranged as in Fig. 12, they collected about 18, that is, once more approximately opposite the light-source. With

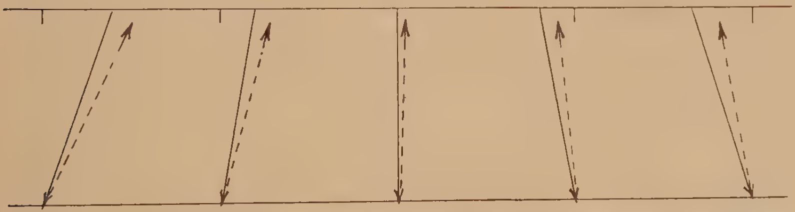

FIG. 15.—Balanus nauplii—paths in light gradient. Continuous line, path of direct light; broken line, path of larvæ.

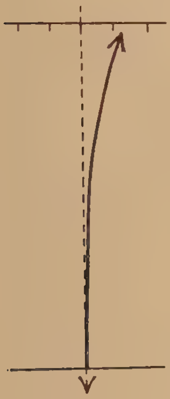

FIG. 16.

Centropages typicus mean direction of path across light gradient.

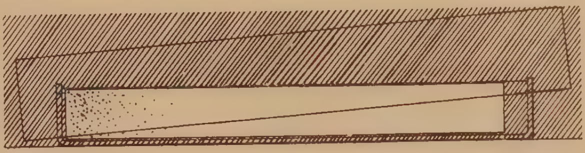

FIG. 17.—*Euterpina acutifrons* in light gradient (see text).

this filter, therefore, there was shown no marked deviation from the path of the direct light; though it should be added that the average paths of individuals placed in the dark end (at 5) or opposite the light (2) seemed consistently to show a slight trend to the right of the order of 1 cm.

By contrast, a very noticeable deviation towards the brighter end was found when Indian ink was placed in the filter. Six different mixtures of increasing concentration were tried in turn. No. 1 mixture was just strong enough to give a perceptible gradient; while no. 6 so dense that the filament of the electric bulb was only just visible in the darkness of the left-hand end of the dish, and it was only the right-hand third of the dish that received any appreciable illumination. No. 2 was twice the concentration of 1, 3 twice that of 2, while 4 and 5 were intermediate between 3 and 6. In each case a group of Euterpina were given adequate time to form a cluster opposite the light, and the position of the midpoint of the cluster was recorded. In each case, also, active specimens were introduced opposite the light-source and the trend of their movement observed. The results, which are graphically shown in Fig. 18, A to F, are as follows :—

Solution.	Midpoint of photopositive cluster.	Deviation to right.
1	27	2
2	28	3
3	30	5
4	31	6
5	37	12
6	39	14

The figures also show the trend of the paths of specimens traversing the dish. In all cases, when starting from 25, they veer towards the point at which the group is formed. The mean path is at right angles to the length of the dish only when the animals are liberated opposite the centre of the group.

The point clearly brought out is that, as the thickness of the filter increases, so the direction of the animals' movement deviates increasingly from the path of the direct light, until a stage is reached at which the animals are, so to speak, driven far into the brighter end of the dish.

It should be pointed out that there is no question of the animals becoming negative to light in the lower intensities. Some tests were made with the same animals used in this experiment and it was found that the animals remained sensitive to light of very low intensity, reacting positively all the time. Moreover, any possibility of the animals having become negative or desensitised during the experiment is entirely annulled from the fact that the animals continued to cluster on the side of the vessel facing the source. Negative animals would have grouped on the opposite side, while desensitised animals would not have formed clusters at all.

It is noteworthy that even in the condition shown in Fig. 18F, the brighter (right-hand) corner is avoided by the animals. The group does not extend into it. By this fact we are assured that the animals are still not grouping in the region of highest light-intensity as such, any more than in other cases.

In respect to the light conditions to which the animals in the dish were subject, it is important to emphasise that the ink suspension in the filter has a considerable scattering effect on the light, thus increasing the amount of diffuse light at the expense of the direct. One would therefore expect the paths of the animals to show more deviation with Indian ink in the filter, than with a clear solution such as ammonia copper sulphate. The deviation would necessarily become greater as the thickness of the solution increases. A further point is that the filtered light becomes

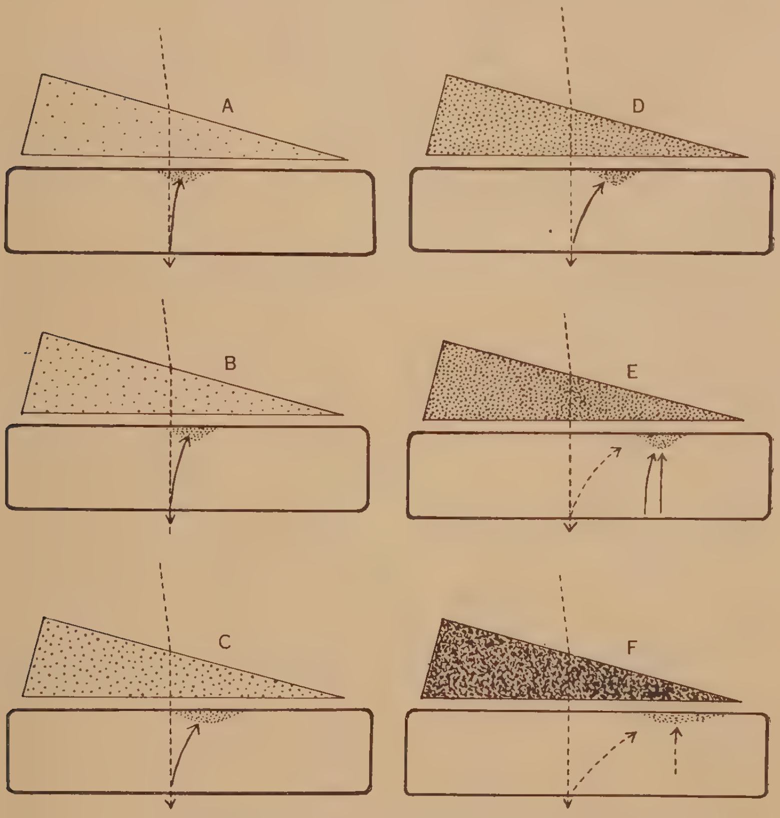

FIG. 18, A to F. *Euterpina acutifrons*—mean paths and groupings in light gradient with increasing concentration of filter.

increasingly redder the more it is absorbed: it gets more and more reddish from the brighter end of the gradient to the dark. Since the Euterpina are presumably less sensitive to this than other parts of the spectrum (some experimental evidence on this was obtained), the gradient will, if anything, be accentuated from their point of view. And such accentuation would tend to increase the deviation of their paths.

After the above considerations it is sufficiently clear that the cause of the deviation is the excess of diffuse light coming from the right-hand side of the dish. In Fig. 18F, it is particularly obvious that an animal, moving in a path in which illumination on its two sides is balanced, if starting in the middle, will move diagonally across the dish towards the region where the group actually formed. There is no question here of the significance of the diffuse light coming from the brighter end of the dish. The other conditions in the Figs. 18E, to 18A, differ from this case only in degree. By gradual stages the importance of the diffuse light diminishes, and we see the accompanying decrease in the deviation of the animals' paths and centre of grouping.

These results are treated in some detail as they provide an explanation of the discrepancies in the work of some previous investigators who have used graded filters (see p. 424).

Balanus (?) balanoides nauplii. Some observations were made on batches of the latest nauplius stage of Balanus, and the results fit in well with those described above. The filter contained a fairly concentrated solution of ammonia copper sulphate, and the dish was placed as in Fig. 13. The procedure in this case was to place pipette-fulls of larvæ at various points along the side of the dish furthest from the light-source, and to note the mean point of arrival on the opposite side.

In crossing the dish the group continuously spread fanwise. The animals reached the opposite side (AB) over a stretch of a few cm. But they were most numerous about a half-way point, which could be readily determined to the nearest ½-cm. This point is given in the table below. It represents the average of three trials.

The results are shown in Fig. 15 and in Table III. It is to be noted that the path is all the time deviated to the right-hand side of the course of the direct light-rays. The right-hand side is the side towards the brighter end of the gradient. The amount of deviation tends to increase towards the brighter end. When left undisturbed the larvæ were found to congregate in the middle part of AB, the centre of the group being slightly to the right of the point nearest the source of light (25). With Balanus nauplii, then, a constant deviation is found, which is no doubt to be ascribed to the same cause as noted above, i.e. scattered light from the bright end of the gradient.

TABLE III.

SHOWING DIRECTION OF MOVEMENT OF BALANUS NAUPLII ACROSS LIGHT GRADIENT.

Point along CD.	Deviation of path from perpendicular (cm.).	Deviation of direc light from perpendicular (cm.).
5	5½ to R.	4 to R.
15	3 ,,	2 ,,
25	½ ,,	0 ,,
35	1 to L.	2 to L.
45	2 ,,	*3½ ,,

Caligus rapax ♂. An actively photopositive specimen gave particularly clear results in the light gradient (apparatus as in Fig. 13 with ammonia copper sulphate solution in the filter). Crossing the dish rapidly, orientated dorso-ventrally, it moved in a straight course which corresponds well with the direction of the light. It then worked its way along the edge of the glass in a comparatively short time and stopped in the region nearest the light-source. For some time afterwards it remained in the latter region. Its behaviour was in exact accord with the expected behaviour of an animal moving in the direction of the light irrespective of the change of intensity, and thus resembled that of the two species already considered.

When the animal swam on its side, the same menotactic behaviour was observed as noted above (p. 397).

Larvæ of the herring (*Clupea harengus*). Considerable difficulty was encountered in obtaining clear results from these larvæ, owing in the first place to their tendency to lose activity and ability to orientate well in low intensities of light. But a further complication appeared in the first trials. Active specimens taken from a positive group and placed in the region of C (Fig. 13) first moved, as expected, across the dish approximately in the direction of the light-rays, and then proceeded to work their way along BA towards the centre of the dish. But instead of remaining in the centre they continued to work their way to A. Before long, all active specimens had collected in the dark end of the dish, the majority clustered around D. The procedure was repeated several times, all precautions being taken to eliminate any source of light that might attract positive specimens to corner D. But the results were consistent. Soon the explanation became apparent —most of the larvæ in the darker part of the dish had become *negative* to light. (That herring larvæ become negative to light of very low intensity was found on other occasions also.) So the only chance of making a successful test with this species was to obtain specimens that had become more adapted to light of low intensity. These were found among larvæ a few days older that were still fit and active. Though it was impossible to reduce the characteristic element of randomness in their movement (see p. 398), the results obtained with them were satisfactory. They moved across the dish roughly in the direction of the light and grouped along AB on either side of the centre line. The group was widely spread, but not enough to give reason for doubt that the bright end as well as the dark end were being avoided. It was quite clear that, in so far as they exhibited phototactic movement, they followed the direction of the light and did not select the region of highest intensity. Their behaviour therefore is essentially similar to that of other phototactic plankton animals treated here.

Observations on behaviour in the light gradient of several other species, to be mentioned below, were obtained. In all cases the same characteristics were to be seen, namely, movement across the dish in a course approximating to that of the light rays and grouping at the region nearest the light-source. Deviations of the kind described for Centropages and Euterpina were noticed as often as they could have been expected to show.

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* Repeated with extra precautions to eliminate scattered light from the sides of the apparatus. The result was the same.

Acartia clausi grouped somewhat to the right of the path of the direct light (apparatus as in Figs. 12 and 13 and dilute Indian ink in filter). *Corycaeus anglicus* swam in a characteristic straight course, but there was considerable variation in the direction of the course taken in different trials. Individual paths of *Paracalanus parvus* also showed variation in direction. This species, at the same time as Acartia, showed tendency to group to the side of the path of direct light (Indian ink in filter). A small Turbellarian moved across the dish in a direct, slightly undulating, path, and gradually worked its way to the region opposite the light-source ; as did also a Polychæt metatrochophore (apparatus as in Fig. 13 ; ammonia copper sulphate in filter). Other forms include : *Temora longicornis*, Balanus larvæ, Zoea larvæ, Copepod nauplii, an Autolytid bud with eggs, and some Mollusc larvæ.

Thus, again, all photopositive animals tested showed the same general behaviour.

BEHAVIOUR OF PHOTONEGATIVE SPECIMENS.

The influence of the direction of the light is particularly well shown by photonegative animals. As ROSE (1925) has noticed at Roscoff, negative specimens in jars of plankton are far less plentiful than positive. And especially is this the case in the low light intensities of the laboratory. The following species are included among the animals that have been studied : *Centropages typicus*, *Calanus finmarchicus*, *Temora longicornis*, and Balanus nauplii, as well as the small bottom-living Harpacticoid, *Nitocra typica*.

In divergent light, it is characteristic that negative specimens of the animals considered in this paper move away from the source, the mean direction of the course taken being along the path of the light rays. If a beam is passed through the water, animals collected at the light source swim down the beam to the opposite side of the dish, and do not immediately pass to the darker regions. This may be illustrated by the paths taken by negative *Temora longicornis*, swimming slowly and steadily, orientated away from the source (Fig. 19).

In a parallel beam (apparatus as in Fig. 1), Temora showed similar behaviour, travelling down the beam away from the source. The specimens tested were moving somewhat irregularly, and the course taken was consequently rather twisty, but the mean direction was straight in line with the path of the light. Not until after reaching the wall of the dish opposite the source did random movements take them into the darker parts of the dish to the sides of the beam. An excellent example of the same behaviour was provided by some negative *Calanus finmarchicus*, which, tested individually, swam straight down the beam with steady uniform motion.

The small Harpacticoid, *Nitocra typica*, a strongly negative species, taken from a bowl in which Amphipods were being reared, also swam down the beam, quite rapidly. The body sways continually, so that the anterior end is always moving from side to side through a wide angle. They first accumulate at the side opposite the source, and then gradually, through the random component of their movement, work their way to the edges of the beam and into the darker parts of the dish.

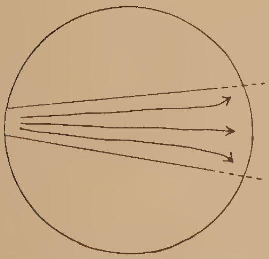

FIG. 19.—*Temora longicornis* —direction of movement of negative specimens in beam passing through circular dish.

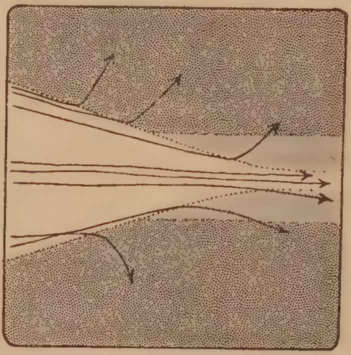

FIG. 20.—*Nitocra typica*—paths in convergent beam.

More instructive still is the behaviour in a convergent beam. *Nitocra typica* may be considered first, as numbers were examined at a time. The mean direction of the paths followed is represented schematically in Fig. 20. It will be seen that, so long as the animals remain in the beam, the course followed inclines towards the centre of the dish, while as soon as random movement happens to take the animal clear of the beam, the course bends abruptly to one side. This is just what is to be expected if the direction of the light-rays is followed, and is, indeed, exactly the type of figure that is obtained from photopositive specimens (Fig. 4), only the movement is then towards, instead of away from, the source.

Temora longicornis gave precisely similar results, the individual paths approximating closely to the ideal. They swim in the direction of the rays, and either enter the narrowest part of the beam, or if they approach the edge before this, turn and swim away to the side of the dish. So too with *Centropages typicus.* Again, *Calanus finmarchicus* swim down the beam in the same way, and show no hesitation on entering the brightest region. Several were observed moving steadily, in a perfectly straight course, following the path of the rays.

Comparable results have been found by KALMUS (1931) to be given by the negative larvæ of *Sabellaria spinulosa.* The latter move down a convergent beam away from the source and concentrate towards the brightest region.

Behaviour in the light gradient (arranged as in Fig. 13) was studied in the case of *Nitocra typica.* Specimens placed anywhere along the edge of the dish facing the light (Fig. 21, AB) move across to the opposite side, their course on the average approximating to the direction of the light-rays. (It cannot be said whether deviations such as have been found for some positive forms occur.) Then they gradually congregate towards the right or the left-hand corner, according to which side of the middle line (where the light passes directly across the dish) they may happen to be. There is no congregation in corner A, although the intensity here is scarcely greater than at D, and very much less than at C : the importance of the direction of the light is once more apparent.

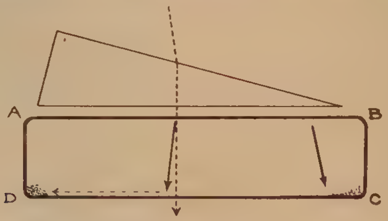

Fig. 21.—*Nitocra typica*—mean paths and groupings in light gradient. Corners of dish marked ABCD.

Thus, in all cases studied, the course of negative movement is found to be the exact opposite of that of positive. It would appear that the same orientating mechanisms are involved in both. And just as positive specimens will move into lower intensities as they approach the source, so too negative specimens will move into higher intensities in travelling away from it. The importance of the direction of the light is shown by the fact that negative animals do not take the most direct route to the darker parts of the dish.

SUMMARY OF PREVIOUS WORK.

I. Phototaxis.

In the foregoing section examples are given of phototactic behaviour observed in marine plankton animals. Examination of the literature reveals a considerable number of scattered records of such behaviour. The better attested of these may now be summarised.

COPEPODA. That many Copepods show positive or negative movement to light has long been known (LOEB, 1893; FRANZ, 1911; ESTERLEY, 1919; ROSE, 1925). No attention had, however, been paid to the paths followed by individuals until FRIEDRICH (1931) described observations on the behaviour of *Calanus helgolandicus* and *Corycaeus anglicus* in parallel beams of light.

CIRRIPEDIA. The phototaxis of the nauplii of Balanus species has for some time been a favourite subject of investigation (GROOM and LOEB, 1890; MOORE, 1909; EWALD, 1912; ROSE, 1913, 1925). But even with these animals the small size has prevented exact study of the "mechanism" of the behaviour.

MALACOSTRACA. The larvæ of *Palæmonetes vulgaris* have been found to move straight to the light source (G. M. WHITE, 1924); so too the strongly reactive Zoeas of *Maia squinado* (Rose, 1925) and the larvæ of *Pinnotheres maculatus* (WELSH, 1932).

PROTOCHORDATA. The tadpole larvæ of Amaroucium species move directly, in a close spiral, towards a source of light (MAST, 1921), the orientation apparently being effected by regular shock-reactions in the way Jennings had supposed for Euglena, and not by topotaxis in the true sense. Amphioxus is described by G. H. PARKER (1906) as being negatively phototropic.

PISCES. FRANZ (1910) found that phototactic behaviour is shown to a greater or lesser extent by various fish larvæ, particularly in small vessels, *Cyclopterus lumpus* and *Trachinus vipera* being among the most reactive. There are other records of certain fish larvæ collecting towards a source of light, or the reverse; but little, if anything, appears to have been done by way of analysing this movement.

MOLLUSCA. The larvæ of the squid, *Loligo pealii*, move straight towards a light-source (G. M. WHITE, 1924).

ANNELIDA, etc. Phototaxis has been recorded in Polygordius larvæ (LOEB, 1893), and Spionid larvæ (ROSE, 1925). *Tomopteris helgolandica* are predominately negative (ROSE, 1925). The negatively phototactic larvæ of *Sabellaria spinulosa* have been studied in some detail by KALMUS (1931).

PLATYHELMINTHES. *Cercaria floridensis* moves in the direction of the light (MILLER and McCOY, 1929).

CŒLENTERATA. YERKES (1903) mentions that the Medusa, *Gonionema murbachii*, when moving upwards in the water, was subject to the directive action of the light. MURBACH (1909), however, criticises this statement, and is of the opinion that the animal never reacts to the direction of the light, but only to changes in intensity.

There are various other instances in which mention is made of positive or negative reaction without further particulars on the relation of the course of movement to the light conditions : e.g. negative ♀♀ of *Labidocera æstiva* (G. H. PARKER, 1901) ; positive Cyprid larvæ of Balanus (VISSHER and LUCE, 1928) ; Sagitta species (ESTERLEY, 1919).

It may be noted that in several cases the phototactic behaviour has been used as a basis for the elucidation of more special problems involved in light response. Thus LOEB and NORTHROP (1917) used Balanus larvæ for testing the validity of the Bunsen-Roscoe law of resultants in reactions to two sources of light; WHITE (1924) observed the distribution of *Palæmonetes vulgaris* and *Loligo pealii* in crossing beams of different monochromatic lights ; VISSCHER and LUCE (1928), in an admirable piece of work, examined the relative stimulating effects of different wave-lengths by a somewhat similar method in the Cyprid larvæ of Balanus ; while WELSH (1932) has measured the effect of temperature and different light-intensities on the rate of swimming in Pinnotheres larvæ. Further, a good deal has been done on the external agencies effective in reversing the " sign," or direction, of taxis (particularly LOEB, 1893 ; ROSE, 1925).

These references should serve to add further evidence to the widespread prevalence, among the smaller free-swimming marine organisms, of phototactic movement ; or, at any rate, of the capacity for such behaviour. One important reservation appears necessary, namely, that this generalisation should, at the present state of knowledge, be restricted to bi-laterally symmetrical animals. It is quite doubtful how far radially-symmetrical animals, such as Medusæ, are influenced by the direction of the light. No experiments on Medusæ are here recorded, partly because they do not survive well, but chiefly because they are not disposed to phototaxis in the manner of other plankton. This, in itself, may be of some significance. Apart from earlier observations on *Gonionemus murbachii*, there is no help to be obtained from past literature.

With regard to the occurrence of more unusual methods of orientation during phototaxis, two examples among Arthropods may be recalled. In the fiddler-crab, *Uca pugnax*, strong positive movement towards a light-source is shown. The animal, however, is all the time orientated sideways (HOLMES, 1908). A case somewhat comparable with *Acartia clausi* is provided by the freshwater larva of the fly *Corethra plumicornis*, which under certain conditions moves in the direction of the incident light, locomotion being accomplished by a succession of jerks in a direction oblique to the axis of the body at the phase of rest. Movement to light occurs because the jerks are predominately to the most illuminated side, and thus are, on the whole, successively to right and left. Thus only accidentally does the animal come to orientate its body exactly in the direction of the light, which, nevertheless, is the average direction of its path.

II. Analysis of Phototaxis.

Very little experimental work has hitherto been published which may help to elucidate the exact nature of the light responses of the animals with which we are concerned. The publications to which reference has been made in the previous section contain only two in which analysis of the phototactic movement has been carried to any length. One of these (KALMUS, 1931) requires further mention, as the experimental methods are of the same kind as those adopted in the work described here. The negative movement of the larvæ of *Sabellaria spinulosa* was investigated. The behaviour of the larvæ was observed in a convergent beam, between two sources of light, and in a light gradient produced by a wedge-shaped filter. The results are in complete agreement with those obtained here with negative forms (p. 418); and they are such as to satisfy the investigator that the movement is definitely a *topo*taxis, and not some kind of *phobo*taxis.

Reference should also be made to a contribution by M. GOLDSMITH (1921), who observed the behaviour of some typical marine plankton animals under the conditions of a light gradient. From the results of this and certain other experiments, she concludes that the reaction to light of these animals is essentially a matter of random movements which bring the animals into a brighter region, and not of orientation to the direction of the light-rays. This is directly contradictory to the results and conclusions stated here, and so requires careful examination. There are good reasons for believing the interpretation to be fallacious, but these are best stated after something has been said of the former work which has involved the use of graded filters.

ON THE USE OF GRADED FILTERS.

Following Strasburger's classical experiments on the swarm-spores of Algæ (STRASBURGER, 1878; and see ROSE, 1929, p. 15), several workers attempted to apply his method on other photoreactive organisms. The main object was to obtain a gradient of intensity in a contrary direction to the incident light, and to discover whether the animals still moved in the path of incidence, or whether they moved up the gradient towards an optimum intensity. At that time "phototaxis" and "photopathy" were the terms used to describe these alternative forms of behaviour, though the latter expression was susceptible of more definitions than one, and very loosely employed. The term "phototaxis" is now used in a wider sense to include all kinds of movement in relation to light, and the sense in which the term was contrasted with " photopathy " is that conveyed in the expression " photo*topo*taxis."

It seems generally recognised that the results obtained by use of this method have not attained the desired objective. In certain cases, notably among Protista and Crustacea, the organisms appeared to be responsive to the light gradient irrespective of the direction of the rays, and so to exhibit " photopathy." But these cases are each open to suspicion, and indeed have been subjected to criticism both at the time by workers in the same field and by later investigators, such as ROSE (1929). It seems that not only are we without sufficient evidence that " photopathic " behaviour does in fact occur, but, if it does, it may be often open to question whether the light gradient in use could adequately show it. The essential difficulty is that the animals concerned may always be capable of moving in the direction of incidence, and experimental conditions have to be very carefully devised to ensure that, while a sufficiently steep gradient is obtained, apparent " photopathic " effects are not produced as a result of behaviour that is essentially topotactic. This consideration applies especially to a case, dealt with below, in which marine plankton animals are concerned.

At the same time it is not to be implied that experiments with graded filters can give no kind of positive result. The results, for instance, have distinct value if definite topotactic behaviour is still shown ; for if the animals still orientate accurately in the direction of the rays, and if they congregate away from the brightest end, as close as they can get to the light-source—just as would happen if no gradient existed—then information is provided on two points : (i) on the independence of topotactic response of gradual changes of intensity in the surroundings, and (ii) on the dominance of topotactic behaviour over any phobotactic behaviour that the animal may be capable of showing. The observations described above (pp. 400–418) should be viewed from this aspect.

It has been seen how various planktonic animals behave in a horizontal light gradient, produced by an Indian ink or ammonia copper sulphate filter, and how the behaviour can be explained completely on the supposition that the animals move in the direction of incidence of the light (and see further the discussion on p. 426 *et seq.*). It was found that an apparent irregularity was clearly to be explained as the effects of light scattered and reflected from the brighter end of the gradient. With Indian ink in the filter the latter effects increased as the mixture was made more concentrated, until, under the conditions represented in Fig. 18c, the animals grouped close to the brighter end of the gradient. The disturbing effect of scattered light was also sometimes observed, though to a less extent, with the copper solution in the filter.

These results render intelligible M. GOLDSMITH'S observations (1921). She gives a brief report on the use of a gradient-apparatus, consisting of a dish painted over with black varnish and covered with a piece of smoked glass of graded opacity. No light could enter the dish except through the cover, which thus acted as a graded filter. The dish was placed near an electric light shining obliquely down on it, with the darkest end of the cover nearest the light. Thus the end of the dish nearest the light was situated at the darkest end of the gradient. Goldsmith's results may be quoted in full :—

"Les Convoluta, les Mysis, les zoé de Maia se groupaient en très grande majorité (il faut noter que l'éclairement était assez faible) dans la partie la plus transparente du vase, qui est en même temps la plus éloignée de la source. Pour les Copépodes planktoniques, il en est de même à la lumière solaire ; à la lumière électrique, la région optima se trouve à mi-chemin entre les deux extrémités du vase."

Considering that the smoked glass must have scattered the light very considerably, the result is quite in harmony with the present observations, and accordingly is not in any way inconsistent with the idea that the animals' response could have been purely topotactic. For one would have expected at any rate the zoeas and Copepods to follow in the mean direction of the light-rays, and the fact that they are brought into the brighter half of the vessel is almost certainly due to the effects of scattered light. The above results are thus essentially comparable with those obtained by DAVENPORT and CANNON (1897) with Daphnia, and E. TOWLE (1900) with Cypridopsis. (Both of these investigators deal with light shining on the filter obliquely from above, and in both cases the animals clearly move in the direction of incidence of the light.)

M. Goldsmith, however, felt justified in the conclusion that the reactions to light of the animals she observed do *not* consist in orientation to the direction of the light-rays depending on a symmetrical influence of the light, but in various random movements which bring them into the brightest region. This verdict is remarkable considering that the animals included such strikingly phototactic forms as Balanus nauplii, *Centropages hamatus*, *Acartia clausi*, Zoeas of *Maia squinado*, etc. Actually it is based on two main pieces of evidence : one has already been adequately dealt with by ROSE, who has carried the experiment in question a stage further, and simply demonstrated that the results are otherwise explicable (1929, pp. 152–153) ; the other piece of evidence is from the behaviour in the light gradient, and this, in view of the above considerations, is seen to be invalid.

With respect to other work involving the use of graded filters, especially that on freshwater Crustacea, it seems likely that if the results were considered in the light of the criticism applied above, some of the apparent inconsistency would be removed. It may be legitimately doubted whether any of the so-called photopathic effects (YERKES, 1899; DITLEVSEN, 1907) are anything but the result of topotactic movement. Still it may be significant that YERKES found a complete contrast in the behaviour of *Cyclops parvus* (" phototactic ") and *Simocephalus vetulus* (" photopathic ") under the same conditions.

INTERPRETATION OF THE RESULTS.

It is now necessary to consider what the observations described in this paper, together with previous work along similar lines, may have succeeded in demonstrating. Our procedure, it may be recalled, has been to observe behaviour under different conditions of illumination designed so that the intensity gradient and the direction of incidence bore different relations to one another. In other words, the data include (*a*) conditions of illumination described as a character of the physical environment, and (*b*) the behaviour of the animals *in relation to* (*a*). It is necessary to be clear on this point when, later, consideration is given to the sensory responses of the animals in question; for the light conditions as " appreciated " by the animal may differ considerably from those thus described, owing to the specialisation of the light-receptors.

Where the Groups Form.

The results on pp. 400–418 show that in no case did positive animals group in the brightest region when this was away from the point nearest the light-source. In a convergent beam, groups always settled at the entrance of the beam, and not in the narrowest, brightest, part. Though fewer species have been tested in the light-gradient, the results obtained were quite consistent (p. 418). The group collected away from the brighter end somewhere in the region opposite the light-source, or, more strictly, in the region of the " axial line " at which the direct light from the source passes across the dish at right angles. This " axial line " in the dish can be found in a simple way by interposing a screen with a narrow slit. It is of significance in that it represents the line along which the direct light is equally balanced on both sides (at least as detectable by a sufficiently small photoreceptive mechanism).

It is to be noted, however, that the groups do not usually form exactly round this point, but at a greater or lesser distance towards the brighter end of the dish. It has been seen how this effect is undoubtedly due to scattered light, of which considerably more will come from the brighter end than the darker, depending on the nature and concentration of the solution in the filter. This scattered light will result in shifting the *effective* " axial line " a little way towards the brighter end.

One may speak of an " effective axial line," defined practically in some such way as follows. Supposing suitable methods of measurement were devised, small arrows could be placed in various parts of the dish indicating the direction in which the light falling on the two sides of the arrow is equal in amount. If one imagines that these arrows are liberally distributed and placed in horizontal rows, it is easy to see that in each row, somewhere near the region of the point close to the light-source, one arrow will point at right angles to the long axis of the dish. A line joining such arrows is what is understood by the expression " effective axial line " (see Fig. 22). It may be straight, or somewhat curved, but in any case it will be nearly, if not quite, at right-angles across the dish, a little to the side of the simple straight axial line of the direct light.

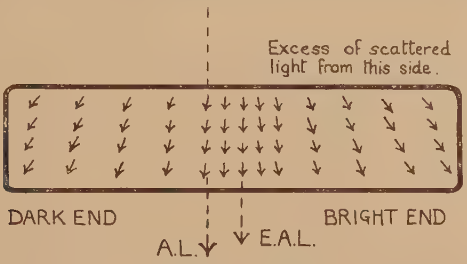

FIG. 22.—Light conditions in light gradient apparatus. At each point the direction of the light is the resultant of two components: (i) direct light from source, (ii) excess scattered light from bright end. A.L., axial line. E.A.L., effective axial line.

We are now in a position to define more precisely the position at which the group forms. If the effects of scattered light were quite negligible, one would expect it to form about the direct axial line ; since, however, they are not, the group instead forms about the " effective axial line." This appears to express adequately the observed behaviour of those animals tested in the conditions of the light gradient.

To state the evidence provided by these results more generally : *positive groups of the plankton organisms investigated primarily collect around a point in the mean line of incidence of the light.* The point in the line will of course be that beyond which the confines of the vessel prevents the animals from passing. *It is immaterial whether this happens to be the brightest region of the dish accessible, or not.* The amount of scattering of the group on either side of the point will vary with the degree of diffuseness of the light. Negative forms show just the expected reverse behaviour.

Behaviour of Individuals.

How the groups come to collect in the above way is explained by examination of the behaviour of the individuals composing them. When the movement of individuals is considered, two points emerge clearly enough.

First, the various animals tested were able to maintain their normal movement in the direction of incidence of the light, whatever the changes of total intensity encountered during their passage. As they moved up a convergent beam, and as they moved towards the axial line in the gradient dish, the intensity was diminishing. The removal of the intensity factor did not noticeably affect their capacity for movement in the direction of the light-rays. Secondly, if the animals have opportunity of " selecting " one of two paths, namely either one of increasing intensity or one in the path of incidence of the light, they will chose the latter.

An animal following the path of incidence will, on the average, maintain an equal balance of the light falling on the two sides of the body, or, strictly speaking, of its photoreceptive surfaces. It is this orientation, exact or approximate, of their path that brings these animals into illuminated regions. They first cross the dish in the path of the rays, and then work their way along the side towards the " effective axial line." The latter phase is naturally the slowest, as the animals are continually moving against the glass, and it is only the excess of random movements in one direction that enables them to progress. At the " effective axial line " random movement in either direction is equally probable ; hence the animals accumulate here. It can now be fully appreciated why the groups form in the positions in which they have been found.

Nature of the Phototactic Movement.

Looking further into the observations on the behaviour of individuals, we may enquire how far the characteristic behaviour of species observed fits into any of the five categories distinguished above (pp. 388–9). This is a matter of more than academic interest, in that if an animal can be assigned definitely to one of these categories, various predictions as to its behaviour become possible. There will, for instance, be an opportunity for speculating what it does in the sea.

In this procedure we are faced with the question, hitherto evaded, as to how the light conditions are to be viewed from the aspect of the animal. So far we have considered the light conditions as a character of the physical environment, for as such they can be measured and described in a straightforward manner. They can be mapped out in a framework representing dimensions of space and time, total intensity indicated by contours and mean direction by a series of arrows. But the simplicity of this scheme is, after all, only because it is, operationally considered, an idealised construction. The specified light conditions of a point within this optical field mean nothing if it is not that they are to be detected by an object placed at that point. And the optical field, described as above, actually represents the conditions of illumination detectable by a hypothetical photometer that is sensitive to light from all directions equally, and is ideally small.

If we regard light-sensitive animals in their capacity of photoreceptive mechanisms, we can discover how they tend to differ from the above-mentioned hypothetical photometer. And we find that the chief difference is that they may by no means be sensitive to light from all directions equally. With motile, bilaterally symmetrical animals, it is generally the case that photoreceptor organs are concentrated at the anterior end and may be largely, if not altogether, shaded from the light falling on the posterior surfaces. Of course the degree to which this happens varies among different forms, but the general tendency is beyond dispute. With such specialised distribution of light-sensitivity over its surface, a photoreceptive mechanism loses its ability to record the changes of light intensity that occur in its surroundings, unless provision is made to allow for its direction of orientation. For now it will record different intensities at the same position according to the direction in which it is facing—as, to take an extreme example, a camera placed at a given point in the beam of a motor head-lamp. We can therefore see, in the first place, how a change of intensity recorded by the animal will be a combination of the change in the physical field and that due to change in orientation of the body in relation to the main source ; and, in the second place, how the resultant direction of the light may also vary—according to the dominance in stimulating power of light falling along the axis of body-orientation over that falling laterally.

All this is to show how the light conditions capable of stimulating an animal as it passes through an optical field may by no means coincide with those reproducible by an ideally small photometer, that is, with the light conditions of the environment stated in physical terms. The animal is here regarded purely in its capacity of an automatic light recorder. It should not, however, be overlooked that further " complications " may be expected from such phenomena as threshold stimulation and state of adaption of the sense-organs ; while, on the other hand, even if the light conditions appreciated may not coincide well with those of the physical surroundings, the behaviour of the animal may be so adapted that its movements will nevertheless be such as to compensate for the difference.

Applying these considerations to the special problem of phototaxis, it becomes apparent that the behaviour observed in the convergent beam and in the light gradient (i.e. direction of light chosen against intensity gradient) is not a conclusive proof of topotaxis (III*a* and *b*, p. 388). It is conceivable that an animal could follow such a path merely by reacting to changes in intensity affecting its sensitive area as a whole owing to small deviations in the direction of orientation of its body, or of its sensitive anterior end. It might all the time be avoiding movement into a position which, to it, involves decrease of illumination. Such behaviour would be classed under (*c*), and justifiably termed *phobotaxis*, although the resulting path the animal follows may be well directed towards the source.

To distinguish this behaviour from true topotaxis is not simple, for in many respects the net result will be identical. But certain distinctions are bound to follow. First may be mentioned a characteristic that provides a useful laboratory expedient for distinguishing between the two types. Unilateral blinding results in circus movements in the first case, not in the second. On these grounds HERTER (1926) has good evidence that *Nereis diversicolor* is enabled through its hind ocelli to move topotactically, but if these are put out of action and the front ocelli left intact, the worm still orientates, though less accurately, by this phobotactic method. In the second place, orientation is evidently more difficult in phobotaxis, and considerable deviations from the mean path are to be expected. Also where movement is not in a spiral path, it is difficult to see how this method of orientation could work at all without considerable side to side movement of the head. It is evidently to be ruled out of the question if the animal orientates accurately towards the source of light and proceeds to move straight towards it without any side movements, as may be observed in the case of most Copepods and various larvæ of Decapods. A further consideration is applicable to an animal which can maintain a fairly well directed path phobotactically; for it follows that the light intensity it appreciates varies greatly with the position of the body. If it should happen to move into an intensity that is too strong, it has only to turn its body slightly to the side to reduce the appreciated intensity considerably. It could therefore achieve the same result by merely turning the body as by moving further away from the source. Clearly, then, an animal of this kind would encounter difficulties in keeping within an optimum zone of intensity. Thus, paradoxically, an animal sufficiently sensitive to changes in intensity to maintain a path directed towards a source, would not easily arrive at a region where the intensity is "optimum."

Returning now to the interpretation of the observed behaviour, we may recall that all cases dealt with are to be classed as *taxis* (III, p. 388). We may further state that no behaviour remotely suggesting (*e*) or (*d*), (p. 389) was noticed; and since all the species moved to, or from, the light in a more or less well-directed path, (*b*), too, is of no account. The latter condition is indeed sometimes approached by animals which normally move in a straight course, but which, for some reason or other, are not reacting well.

We are therefore left with alternatives (*a*) and (*c*). Something has already been said of the distinctions between these two modes of behaviour. It may be repeated that any animal maintaining accurate orientation and moving in a straight line in the direction of incidence, with no sideways or " searching " movements, cannot possibly be classed under (*c*). True topotaxis is, therefore, exhibited by :—

various Copepods : *Centropages typicus*
Temora longicornis
Paracalanus parvus
Corycaeus anglicus
Caligus rapax ♂
Decapod larvæ : Galathea spp.
Upogebia sp.
Pandalus montagui
Zoea larvæ of Porcellana sp. and other crabs
Cirripede metanauplius
At least some Polychæt larvæ.

These animals are presumably capable of appreciating differences between light falling on the right and left sides, and of adjusting their position so that the intensity is equally balanced. It is of interest to note that whereas the Decapod larvæ possess paired compound eyes of some size, Calanoid Copepods have but a small single median eye. Yet for slow movement the latter are capable of orientating with considerable accuracy. *Corycaeus anglicus* has large paired lenses focussing on small paired eyes, and it is evident that the light falling straight from the direction in which the animal happens to be facing will be far more effective than that falling laterally or from behind. That this is actually the case is indicated by certain features of the animal's behaviour.

The species in the above list, as well as others, which, as emerges later, should be classed with them, may be expected to exhibit characteristics which appear to be generally typical of topotactic behaviour : for instance (i) ready reversal from positive to negative, and *vice versa*, under the influence of appropriate stimulation, such as temperature change, chemical change, mechanical shock, increase of light-intensity, etc. ; (ii) movement in a diagonal line between two light sources, or movement in the resultant line when the light is falling from various directions or greatly scattered. Such behaviour has actually been tested and observed in several of the above species. *Corycaeus anglicus* is less inclined than others to keep to a diagonal between two sources, owing without doubt to the fact that its lenses are so constructed as to concentrate light from one direction.

It may also be noted that when the light is broken up and made to fall from various directions, the paths are more varied, and the groups formed more scattered, but the average direction of movement approximates to the direction from which the greatest amount of light is coming and on either side of which the total amount of light is fairly equalised.

Two other cases of topotaxis stand quite on their own. First, the strongly positive *Acartia clausi* is, as we have seen, capable of moving in a reasonably straight path in the direction of a light-source, without keeping its body orientated in any fixed direction. Movement is in " jerks," and successive " jerks " are not necessarily in the same direction, so that the course is somewhat zigzag (see p. 396). During movement the body may be orientated in almost any direction, though positions in which the anterior end is above the lower are most frequent. The appearance is as though the animal were being forcibly pulled to the light in whatever direction it attempted to move. The fact that *Acartia* moves likewise in the path of incidence of the light in a convergent beam and across a light-gradient proves that the animal is not reacting to changes in intensity—i.e. its phototaxis is not type (*c*) ; for its transparent body and constant body-orientation ensure that it is affected by light from all directions fairly equally. The movement is thus a variety of true topotaxis, but how exactly this is brought about presents a problem that cannot be answered by the usual interpretations of this category of behaviour. Secondly, *Poecilochaetus serpens*, writhing vigorously, so that no part of its body has any constant relation to any other part, is able to move straight up a beam of light (p. 399). Again we are presented with the phenomenon of orientation of the path in absence of orientation of the body.

It appears, then, a distinction should be drawn between cases of true topotaxis in which orientation of the path is the result of orientation of the body, and those in which it is not. That cases of the latter type should occur at all is of some interest, and the fact by no means simplifies the theory of phototaxis. Perhaps it occurs more frequently than may be suspected. It has been noted (p. 398) how a Pandalus larva moved straight up a beam although orientating at various oblique angles.

The foregoing paragraphs deal with clear examples of true topotaxis (Type *a*), which stand out because of the accuracy with which orientation can be effected. Since a number of such examples occur, one may confidently expect to find along with them many others in which orientation is not so efficient, though effected in essentially the same way. The animals, though exhibiting true topotaxis, will not keep such a straight course. There can be little doubt that the bulk, if not all, of the other species referred to fall into this class. For instance :—

Copepoda : all species in more rapid movement
Euterpina acutifrons
Nitocra typica
Cirripedia : Balanus nauplii
some Polychæt larvæ
Decapod larvæ.

Thus the whole range of species investigated is practically covered ; and the evidence is strong that true topotaxis (*a*) is the primary type of response of these animals to light.

But whatever closer study on the distinction between (*a*) and (*c*) may show, it is for most purposes sufficient that the animals examined fall into one or other of these categories. For it means that all have one important characteristic in common. That is, that the response to light is such that movement is always in the direction of the rays. The influence of the direction of incidence is such that the changes of light intensity encountered during progress are of no significance with respect to direction of movement. That this statement should not be misunderstood, it is perhaps necessary to point out that it is by no means implied that changes of intensity have no influence at all. Such would be contrary to fact. Reactions, for instance, may occur to sudden changes, such as when an animal enters a beam or a shadow ; movement may be activated or inhibited by variation in light intensity, or the direction of phototaxis reversed. And since in nature the animals are subject to sudden shadowing, to fairly rapid changes at dawn and dusk, and to increase in light-intensity as they move upwards in the direction of incidence, such behaviour is undoubtedly of importance. The point, however, with which we are here concerned is that changes in intensity in the environment are of no significance for the maintenance of the sort of phototactic movement that a wide range of plankton animals show. The path of the animal is orientated in the direction from which the light is coming, or, if the light is scattered and falling from various directions, to the resultant of the total incident light. And whether the actual mechanism of this movement is that of class (*a*) or class (*c*), the general course of movement is the same.

These conclusions are based primarily on the observations here described, but they also receive some support from those that are to be found in the literature. It may be pointed out that, in general, observers of the behaviour of plankton animals have been struck by the apparent topotactic nature of characteristic light responses. In particular, reference should be made to M. ROSE (1925, 1929), who has paid as much attention to this subject as anyone. One gathers from his publications that he regards the directional properties of the light as of primary significance. The experimental evidence here provided justifies this opinion.

RELATION TO THE PROBLEM OF VERTICAL MIGRATION.

It is not unreasonable to assume that the animals exhibit the same *kind* of response in the sea as in the laboratory, though the *extent*, or the *intensity*, or the *persistence* may differ in the two cases. If this is so, then movement in the direction of the incident light, whether positive or negative, should at least figure prominently among the light responses of the animals in nature.

Accurate field-work, in which a valuable lead has been given by F. S. Russell, is showing that movements of the plankton are related to changes in the light conditions more readily than to any other environmental factor. Some species, indeed, tend to " follow " an optimum intensity. In so far as this is the case, we can now point to topotactic behaviour as one important means whereby such an " optimum " is reached. Positive topotaxis is of itself sufficient to bring animals from low intensities up towards their " optimum," and may alone be adequate to keep persistently positive forms such as *Acartia clausi* high in the water. When the light-intensity increases beyond the " optimum," one must suppose, in so far as light conditions regulate behaviour, either that the animals become negatively topotactic (Loeb's original theory), or that movement is inhibited and the animals sink back into their " optimum " zone (as first put forward by EWALD, 1912). Be that as it may, the prevalence of the kind of orientated movement to which prominence has here been given, could account in a large measure for the correlations that are found between vertical distribution and light-intensity.

SUMMARY.

1. The most noticeable response of marine plankton to light, under laboratory conditions, is the formation of groups on the lighted (or opposite) side of the vessel containing them.

2. Specimens from such groups were tested under different conditions of illumination, and in all cases they moved in the *direction* of the light quite irrespective of accompanying changes of *intensity* in the surroundings.

3. Groups form around the line of direction of the light, or the resultant direction when the light is scattered or falling from more directions than

one, this being the direct result of individuals moving along the mean path of incidence of the light.

4. The behaviour of individuals was examined more closely to distinguish between the two possible ways in which the directed movement could have been brought about, viz. (i) reactions to bilateral inequalities of illumination (here called "true topotaxis"), and (ii) reactions to changes in total illumination of light-receptors (a type of "phobotaxis"). For a number of species it was clearly a case of "true topotaxis," and very probably for at least the majority of the rest.

5. In two very different cases, namely, *Acartia clausi* and *Poecilochaetus serpens*, there was no orientation of the body, but nevertheless efficient orientation of the path of movement. It is believed that this is the first occasion on which such behaviour has been described.

6. The observations described point to the fact that movement in the direction of incidence of the light, however this may be affected, is general among a wide range of the smaller, free-living, bilaterally symmetrical, marine animals, and would tend to dominate other possible response to light. This behaviour on the part of individuals provides a substantial basis for attempted explanations of the correlations, that have been demonstrated by ecological workers, between the vertical distribution of populations and light-intensity.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

The Loxosomatidæ of the Plymouth Area, including *L. obesum* sp.nov.

By D. Atkins.

Quart. Journ. Micr. Sci., Vol. LXXV, 1932, *pp.* 321–391.

Four known species of Loxosoma, *L. phascolosomatum* Vogt, *L. crassicauda* Salensky. *L. singulare* Keferstein, and *L. claviforme* Hincks, and a new species *L. obesum* found in the Plymouth region, are described.

In *L. crassicauda*, which lives in the tanks in the Laboratory, males only were found during the year they were kept under observation.

L. claviforme is considered a valid species.

A small group of Loxosoma, found on *Aphrodite aculeata*, were intermediate in form between *L. singulare* and *L. claviforme*, and peculiar in retaining a number of their buds. The sex of such buds in several instances differed from that of the parent.

L. obesum sp.nov., found on the dorsal surface of *Aphrodite aculeata*, may reach a length of 2·4 mm., and averages rather more than 1·0 mm. in length. The lophophore is small, and bears almost invariably eight tentacles. Longitudinal muscles only are present in the stalk, which ends in a small disc of attachment. A foot-gland is present in the bud, and is frequently preserved as a vestige in the adult. The buds are near the lophophore, and may be as many as six on each side. The larva resembles that of *L. singulare.*

Two main forms are distinguishable, differing in shape of the calyx and development of the stomach.

The ovary may contain six well-developed ova on each side, and the vestibule twenty-six embryos.

Females, with one exception, greatly exceeded males in number, and it is probable that the male becomes sexually mature at a smaller size than does the female.

D. A.

The Ciliary Feeding Mechanism of the Entoproct Polyzoa, and a comparison with that of the Ectoproct Polyzoa.

By D. Atkins.

Quart. Journ. Micr. Sci., Vol. LXXV, 1932, *pp.* 393–423.

An account is given of the ciliary feeding mechanism of the Entoproct Polyzoa, and of the structure of the lophophore and tentacles. The long lateral cilia cause a current of water to pass inwards between the tentacles, and throw particles on to the short frontal cilia of the inner surface, which carry them to the vestibular groove leading to the mouth.

The behaviour of the lateral cilia of the tentacles of *L. crassicauda* is described, and it is suggested that they are under the nervous control of the animal.

A résumé of Borg's work on the ciliary feeding mechanism of the Ectoprocta is given, a note on *Flustrella hispida* being added. It is pointed out that the method of feeding in this group differs widely from that of the Entoprocta.

D. A.

The Nematode Genus *Ascarophis* van Beneden.

By H. A. Baylis.

Ann. & Mag. Nat. Hist. (10), *XI*, *pp.* 111–117.

Two female specimens obtained from the stomach of a gurnard (*Trigla lineata*) at Plymouth are referred to the very imperfectly-known species *Ascarophis morrhuæ* van Beneden, 1871, which had been recorded previously from the cod, haddock, halibut, and father lasher. The literature dealing with this species and with *Ascarophis helix* Cobb, 1928, is reviewed. In the light of the present material the description of the female is amplified (the male being unknown), the doubtful systematic position of the genus is discussed, and an emended generic diagnosis is given.

H. A. B.

The Osmotic Relations between White and Yolk in the Hen's Egg.

By J. B. Bateman.

Journ. Exp. Biol., 9, 1932.

Vapour-pressure determinations on white and yolk of the hen's egg, (*a*) by direct comparison, (*b*) by reference to an intermediate salt solution, and (*c*) by dialysis against known salt solutions, have confirmed the existence of a real osmotic difference between these two substances. These experiments show A. V. Hill's vapour pressure thermopiles to be reliable when used with viscous protein solutions such as egg yolk, and that a recent criticism is unfounded.

The vapour pressure changes which occur on mixing white and yolk indicate a removal of osmotically active substances; they disagree, therefore, with Straub's freezing-point determinations (1930). Dilution of white and yolk with water and with various salt solutions is studied from this point of view and also in connection with the problem of bound water. It is concluded that the amount of bound water in both white and yolk is small, and this is confirmed by the effect of solid sodium chloride on the vapour pressure of white and yolk. Other substances (urea, sodium lactate) produce abnormal effects resembling their effects on blood. Glucose behaves normally.

The result of mixing white and yolk, mentioned above, is discussed in relation to the osmotic changes occurring in the fertilised and unfertilised egg.

J. B. B.

The Heat Production and Economy of Maintained Contractions in Crustacean Muscle.

By D. W. Bronk.

Journ. Cell. & Comp. Physiol., II, pp. 285–294, 1932.

The heat production of crustacean muscle has been measured during the course of a short tension by means of a single thermocouple thrust into the adductor muscle of the claw of Maia. It has been found that there is a marked increase in the economy of maintaining tension, as represented by the ratio of tension developed to heat produced, as a result of previous activity of the muscle. This striking increase in economy is shown to be due to a very marked slowing of the muscle as a result of previous contractions. The slowing is very much greater in this type of muscle than in vertebrate striated muscle. It is pointed out that this would make it possible for the animal economically to maintain powerful contractions for considerable periods of time in spite of the fact that the motor nerve fatigues rapidly, as has previously been shown to be the case by A. V. Hill.

D. W. B.

The Effect of Veratrine on the Electrical Response of Crab's Nerve.

By S. L. Cowan.

Jour. Physiol., 77, 27*P.*

After soaking for half an hour in aerated sea water (pH 8) containing 1 in 10 millions to 1 in 100 millions of veratrine, a nerve from a walking leg of Maia gave a much increased initial action current, as measured with a galvanometer of 3·8 sec. period.

For autumn crabs the optimum concentration of veratrine was 1 in 25 millions to 1 in 50 millions; the initial response was about 200 times that of untreated nerve and the area of the deflection × time curve was increased more than a hundredfold. The "retention of action current" lasted for nearly half an hour.

Asphyxiation, previous to stimulation in oxygen, did not affect the response. (Compare Fromherz, H., and Hill, A. V. *J. Physiol.*, 77, 25 P.)

S. L. C.

Note on the Occurrence of *Graffilla gemmelipara* Linton (Turbellaria) at Plymouth.

By W. Harold Leigh-Sharpe.

Parasitology, Vol. XXV, No. 1, 1933.

On 28.viii.1932 seven specimens of *Graffilla gemmelipara* Linton 1910 were found by Miriam Rothschild on the body inside the mantle cavity of a specimen of *Cardium edule* from Millbrook, Plymouth.

Though only taken previously in America and on a different host, *Modiolus plicatulus*, Linton's excellent figure leaves no doubt that these specimens belong to the same species.

The mother, a perfect oval, is uniformly ciliated, colourless and transparent, with a pair of typical Turbellarian bean-shaped eyes, and contains within her body eight bubble-like, transparent, spherical cysts. Each of these contains a pair of ciliated young, complete with eyes like their mother ; and the young of each pair are arranged head to tail and slowly revolve within the cyst. W. H. L.-S.

A Second List of Parasitic Copepoda of Plymouth with a Description of Three New Species.

By W. Harold Leigh-Sharpe.

Parasitology, Vol. XXV, No. 1, *pp.* 113–118, 1933.

The following constitutes a supplement to my previous list (Leigh-Sharpe, 1926), and consists of a few records previously omitted, and also an account of some Copepoda taken by me during a visit to the Laboratory of the Marine Biological Association, Plymouth, Aug.–Sept. 1932, with notes on these and previously recorded species. Three new species are described : *Lernæocera phycidis*, *Clavella deliciosa* and *C. typica*, and an account of normal and abnormal specimens of *Lernæocera lusci*. Notes are given on the eggs and nauplii of the Dichelesthiidæ. W. H. L.-S.

On the Mitraria Larva of *Owenia fusiformis* Delle Chiaje.

By Douglas P. Wilson.

Phil. Trans. Roy. Soc. B., Vol. 221, 1932, *pp.* 231–334.

This is a detailed histological study of the development from the early trochosphere to the young worm a few days after metamorphosis. The larva is of a most unusual type, in which the normal mode of Polychæte development is masked by an exaggeration of some larval structures associated with a peculiar disposition of certain parts of the developing worm trunk. The prototroch beginning as a simple ring becomes folded into a sinuous tract simulating the ciliated band of an Echinoderm larva. The blastocœl is spacious. Long provisional bristles probably protect the larva during its month of pelagic life. The worm trunk develops in such a way that the anterior segments are turned inside out and are folded back to envelop the posterior segments. The head is widely separated from the trunk, but is connected with it by the circumœsophageal nerve commissures and by a pair of retractor muscles, as well as by the larval tissues of the blastocœl wall. The development culminates in a metamorphosis of cataclysmic violence and rapidity in which during the course of a few seconds the trunk is straightened out while the head is drawn down on to its anterior end and there subsequently fuses with it. The provisional bristles are thrown off and lost, but the softer larval tissues—the prototroch and other structures—break down in rapid histolysis and are swallowed by the newly-formed worm during the first few minutes of benthonic life. Laboratory experiments indicate that in the sea it is usual for this metamorphosis to take place only when the fully developed larva comes into contact with a suitable sandy bottom, and that it is delayed for a time if the larva has not reached the sea-bed or if the bottom conditions are unsatisfactory. Such a power of suspending metamorphosis must greatly add to a larva's chance of ultimately reaching the right kind of bottom for adult life. D. P. W.

The Autonomic Nervous System of Selachians.

By J. Z. Young.

Quart. Jour. Micr. Sci., Vol. 75, *p.* 571.

An analysis of the visceral motor nerves of Selachians was made, with a view to comparison with the arrangement in mammals. Very little evidence was found of the existence of functionally antagonistic sympathetic and parasympathetic systems, and it is suggested that these systems in Tetrapods represent specialisations within a single segmental set of visceral motor fibres, running primarily through the dorsal roots, but coming to pass through the ventral roots in those segments in which the roots join.

In the trunk region of Selachians the rami communicantes contain only pre-ganglionic fibres, i.e. there are no grey rami, and in accordance with this it was found that the melanophores of the skin are not innervated.

The structure of the autonomic neurons is described in detail. In the case of the post-ganglionic cells which innervate the suprarenal bodies the processes can sometimes be followed all the way from nerve cell to nerve ending so that the hypothesis of Elliott, that the chromophil cells themselves represent post-ganglionics, is disproved. J. Z. Y.

Comparative Studies on the Physiology of the Iris. I. Selachians. II. Uranoscopus and Lophius.

By J. Z. Young.

Proc. Roy. Soc. London, Ser. B, Vol. 112, *p.* 228, 1933.

It was found that the sphincter muscle of the iris of Selachians is not under nervous control but contracts in direct response to illumination. The dilatator muscle, on the other hand, receives motor fibres from the oculomotor nerve. The action of various drugs on these muscles was then tested and it was found that whereas adrenaline, acetyl choline, pilocarpine and eserine all caused contraction of the dilatator muscle, none of these substances caused any contraction of the sphincter. This is held to be evidence that these drugs act at the mioneural junction and not on the muscle fibres themselves.

Both of the muscles of the iris of Uranoscopus and Lophius are under nervous control and a study of the effects of drugs in these forms gave results in agreement with the above hypothesis. J. Z. Y.

Nervous Degeneration and Regeneration in Cephalopods.

By E. Sereni and J. Z. Young.

Pubbl. Staz. Zool. Napoli., Vol. 12, *p.* 173, 1932.

A study was made of the effects of sectioning the mantle connective or stellar nerves in various Cephalopods. The process of degeneration and regeneration of the nerves is described in detail and an analysis made of functional components of the nerves in question. After section of the mantle connective degeneration proceeds as far as the stellate ganglion but not into the stellar nerves, and this fact demonstrates that there is no continuity between the axons of the connective and the neurons of the stellate ganglion. In agreement with this the actual terminations of the fibres in the stellate ganglion ("boutons terminaux") were recognised, this being the first time that such structures have been described in invertebrates. J. Z. Y.

Notices of Books.

Origin and Environment of Source Sediments of Petroleum. By Parker D. Trask, assisted by Harold E. Hammar and C. C. Wu. Gulf Publishing Co., Houston, Texas, 323 pp., 1932.

This book contains much interesting matter, not to be found elsewhere, based upon the examination of sediments from about 1600 localities from all parts of the world.

The organic content of a marine deposit depends upon the supply of organic matter in the overlying water, due allowance being made for the effects of transportation and decomposition. The importance of the upwelling of deep water rich in phosphates, nitrates and other nutrient salts has been made evident, so that bottom deposits in such regions rich in plankton are themselves rich, save where steepness of slope may hinder deposition ; basins on the other hand are richer in organic matter.

The organic content of recent marine sediments ranges between 0·3 per cent in deep ocean oozes and 7 per cent in deposits of the Channel Islands region of California. Pelagic sediments contain very little organic matter.

In the surface layers nitrogenous components form 40 per cent of the organic matter and lignin-humus complexes comprise 30 per cent. Oils and fats comprise less than 0·3 per cent. Changes take place in the organic matter before the deposits have become consolidated, so that much of the matter deposited disappears. It is considered that petroleum arises owing to the conditions to which the organic matter is subjected after consolidation.

About 130 recent and 30 past sediments were distilled in iron retorts, the results being remarkably alike. The oil production varies directly with the organic content. In recent marine sediments the maximum yield is 3 gallons per ton and in past deposits 6 gallons. In rich sediments, both past and recent, 25 per cent of the organic matter is converted into oil, but less than 5 per cent in poor deposits. Oil is formed in the retorts between about 260 and 525° C., its specific gravity lying between 0·88 and 0·98. Water and gas, mainly methane and hydrogen, are also produced.

In this work researches in marine biology find a direct application and the results obtained by the authors are of interest to a field far wider than that of petroleum technology.

W. R. G. A.

The Marine Shells of Port Alfred, S. Africa. By Lt.-Col. W. H. Turton, D.S.O. Oxford University Press, London: Humphrey Milford, 331 pp., 1932, Pl. I–LXX, 18s. net.

This is an account of shells collected for many years at Port Alfred. It is valuable because they all came from this one very rich locality, and among them are some hundreds of new species which are figured in photographic plates at the end of the volume. It is the result of an enormous amount of work, but is purely conchological. Apparently no effort whatever was made to discover the form of the animal, natural habitat or general biology, and most of the shells were collected when dead, the numerous minute forms having been obtained by sifting sand.

The wonderful variety of these small shells makes us wish for some good notes on their living inhabitants. Some of the minute new species are almost certainly larval forms, for instance *Trophon ornatus* is much more like a larval Philbertia than a Trophon, having almost the exact sculpture and shape of some of the British species; *Triphora retusa* may easily be still a veliger, and many others of these we should like to see alive before admitting them as new species. M. V. L.

British Museum (Natural History). Instructions for Collectors. No. 12—Worms. 22 pp., 1932, 6d.

This is a new edition of a familiar handbook on the collection and preservation of worms, the latter term being used in its widest sense. It has been thoroughly revised, and is a most attractively produced as well as useful publication. Brief non-technical descriptions of each of the main worm groups, illustrated by nineteen clear and well-chosen illustrations, should help the non-specialist collector in classifying his specimens before looking up the appropriate methods of preservation. The methods given are simple and good, but exception must be taken to the statement that Arrow-worms fixed in Bouin for histological study should be stored in formalin (page 12). It should also have been clearly stated that when Bouin's fluid is used it must be washed out with strong alcohol and not with water, as readers unfamiliar with the fixative will probably assume. The handbook ends with a useful descriptive list of fixatives and instructions as to labelling and packing. D. P. W.

Marine Biological Association of the United Kingdom.

Report of the Council for 1932.

The Council and Officers.

Four meetings of the Council have been held in London during the year, at which the average attendance was sixteen. The meetings were held as usual in the rooms of the Royal Society at Burlington House, and the thanks of the Association are due to the Royal Society for the accommodation provided. A Committee of the Council, consisting of six members, including the Chairman, Professor E. W. MacBride, F.R.S., visited and inspected the Plymouth Laboratory.

The Plymouth Laboratory.

The good state of repair of the Laboratory buildings and fittings has been maintained ; the woodwork of the north building and north side of main building, and the interior of the tankroom have been repainted throughout. Much interior painting of the north building has been carried out by direct labour. The approach from the main gate to the entrance of the building has been levelled and paved with tarred stone.

The motor pump, which was installed in place of the old gas engine, has worked satisfactorily and the circulation of water and air throughout the tanks has proved sufficient.

Extension of Laboratory Buildings.

The new series of laboratories forming an extension of the north building, which have been built through the generosity of the Rockefeller Foundation, who made a grant of £4,642 for the purpose, were completed and taken into use at the beginning of the summer. The new block contains two large laboratories, one for physiology and one for biochemistry, a special room for photographic work and experiments on the effects of light on the reactions of marine animals, and five smaller laboratories for general purposes. It constitutes a most valuable addition of working space, for which the Association is deeply indebted to the Rockefeller Trustees.

The Ship and Motor-Boat.

The steam drifter *Salpa* has been steadily at work during the year, with the exception of the customary and necessary periods in harbour for refit and overhaul. Both hull and engines are in very good order.

The motor-boat *Gammarus* has been in regular use throughout the year and is maintained in sound condition.

The Staff.

The Council desire to congratulate Dr. C. M. Yonge on his appointment to the newly-constituted chair of Zoology in the University of Bristol. Dr. Yonge has done most useful work at Plymouth for a number of years and he will be greatly missed at the Laboratory.

Mr. J. E. Smith's term as Student-Probationer was completed in September and he has since taken up an appointment in the Zoological Department of the University of Manchester.

Mr. O. I. Green of Oxford has been appointed Student-Probationer to succeed Mr. J. E. Smith.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :

MISS D. ATKINS, London (Pinnotheres and Lamellibranch gills).
DR. J. R. BAKER, Oxford (Pharmacology of sperms).
R. BASSINDALE, Middlesbrough (Identification of Tees Estuary Invertebrates).
J. B. BATEMAN, Cambridge (Osmotic regulation in shore crabs).
DR. H. A. BAYLIS, London (Parasitic worms from fishes).
MISS E. D. BEAVIS, Darley Dale (Marine Algæ).
MRS. M. P. BERESINA, Leningrad (Heat production in crustacean nerves).
DR. N. J. BERRILL, Montreal (Ascidian embryology).
MISS A. M. BIDDER, Cambridge (Digestive system of Loligo. Vital staining of Cephalopod larvæ).
MISS M. V. BISHOP, London (Development of Buccinum).
R. BOTO, Lisbon (Chemical Constituents of Sea-water).
PROF. D. W. BRONK, Philadelphia (Fatigue of muscles of Maia through stimulation).
H. A. COLE, Bangor (Morphology of fishes).
S. L. COWAN, London (Chemical exchanges in crustacean nerve).
DR. C. CROSSLAND, Ghardaqa Marine Laboratory, Red Sea, Egypt (General Zoology).
D. D. DASEN, Liverpool and Madras (Fish eggs and larvæ).
J. H. DAY, Liverpool and S. Africa (Plankton. Growth of Crabs and Sacculina).
W. J. R. DEEKS, London (General Zoology).
DR. G. P. EGGLETON, Edinburgh } (Phosphate in crab nerve. Car-
DR. P. EGGLETON, Edinburgh } nosine in invertebrate muscle).
T. P. FENG, London (Heat production in crustacean nerves).
DR. M. FLORKIN, Liége (Hæmerythrin in Phascolosoma).
MISS E. GEORGESON, Leeds (Ascidians).

F. M. Ghazzawi, Liverpool (Histology of intestines of Mullet).
A. Graham, Sheffield (Patella).
J. Gray, Cambridge (Movements of fishes).
O. I. Green, Oxford (Food of fishes. Natural history of *Lepidorhombus whiff*).
Dr. R. Gurney, Oxford (Copepod nauplii).
J. E. Harris, Cambridge (Cinematography of fish movements and eggs of marine animals).
J. C. Hayes, Manchester (Young marketable marine fishes).
H. Henson, Leeds (Development of Haliclystus).
Prof. A. V. Hill, London (Chemical exchange in crustacean nerve. Heat production in crustacean nerve).
Mrs. Greta Hörstadius, Stockholm (Proteolytic enzymes of Aplysia and Helix).
Dr. Sven Hörstadius, Stockholm, Ray Lankester Investigator (Heredity in sea-urchins. Development of Luidia. Phagocytosis in Gastropods).
A. F. W. Hughes, Cambridge (Injection of fishes).
Dr. Walther Huth, Berlin (Ophryotrocha).
Miss P. M. Jenkin, Cambridge, Ray Lankester Investigator (Correlation of photosynthesis of diatom cultures in the sea with photoelectric measurements of light penetration).
E. I. Jones, London (Fish Trematodes).
Dr. T. Kamada, Tokyo (Pedal waves of Gastropoda).
J. A. Kitching, London (Wembury Bay Fauna. Contractile vacuoles of Protozoa).
Mrs. M. K. Krainska, Warsaw (Behaviour of yolk in crab's egg).
W. H. Leigh-Sharpe, London (Parasitic Copepods).
A. G. Lowndes, Marlborough (Movement of sperm in Ostracods).
G. I. Mann, Plymouth (General Zoology).
B. J. Marples, Manchester (Anatomy of the vascular system in Elasmobranchs).
G. A. Millikan, Cambridge (Maia blood).
C. C. A. Monro, London (Polychæte worms).
C. F. A. Pantin, Cambridge (Osmotic control in Amphipods).
L. E. R. Picken, Cambridge (Osmotic regulation in Sipunculids).
Dr. H. H. Poole, Dublin (Measurement of submarine illumination).
P. Powers, Pennsylvania (Parasitic Protozoa in Echinus).
Miss N. Reed, London (Sporozoan parasites in Annelids).
A. D. Ritchie, Manchester (Pecten and Oyster muscle).
Miss M. L. Rothschild, London (Parasitic Trematodes).
J. P. Scott, Oxford and Wyoming (Cleavage of Echinus).
Miss F. E. Smith, Plymouth (Nemertines).
F. G. W. Smith, London (Development of Patella).
S. Smith, Cambridge (Nitrogen excretion of *Carcinus mœnas*).
Dr. E. A. Spaul, London (Relation of the thyroid and pituitary body in fishes).
Miss F. A. Stanbury, Plymouth (Diatom cultures).
Miss E. M. Stephenson, Birmingham (Colour change in Crustacea).
Dr. S. Takatsuki, Tokyo (Physiology of the oyster).
Miss M. J. Thomas, London (Feeding mechanisms).
R. C. Vernon, Plymouth (General Zoology).
Prof. J. Paul Visscher, Cleveland, Ohio (Distribution and periodicity of Cirripedia).
G. P. Wells, London (Action of salts on invertebrate muscle).
Mrs. D. P. Wilson, Plymouth (Marine Algæ).

Dr. Sven Hörstadius of Stockholm was appointed Ray Lankester Investigator, and with his wife, Mrs. Greta Hörstadius, worked at the Laboratory for five months during the summer. Subsequently Miss P. M. Jenkin of Cambridge was appointed to the same investigatorship and commenced work in October.

A meeting of the Society for Experimental Biology was held at the Laboratory in July and was well attended.

The usual Easter Vacation Course in Marine Zoology was conducted by Mr. D. P. Wilson and Mr. G. A. Steven, and was attended by forty-one students from Oxford, Cambridge, London, Edinburgh, Liverpool, Manchester, Birmingham and Exeter.

A Course in Marine Biology was also held during the Summer Vacation, conducted by Prof. J. H. Orton, of Liverpool University, and was attended by fifteen students from Cambridge, London, Liverpool, Exeter, and Portsmouth.

During the Easter Vacation, Mr. J. M. Branfoot brought five students from Oundle School, one from Clifton College, and one from Winchester College; Mr. M. W. Barr, three from Harrow; Dr. E. W. Shann, eight from Rugby, two from Stowe School, and one from Wellington College; Mr. H. P. Ramage, three from Gresham School; Mr. C. T. Prime, two from Whitgift School; Mr. I. Hamilton, one from Dauntsey School; and Mr. H. C. Wilson, three from Monkton Combe. Mr. A. S. Gillespie and Mr. A. S. Turner, from Rydal Mount School, Colwyn Bay, also came as visitors.

At Whitsuntide Mr. E. I. Jones of the Chelsea Polytechnic conducted a class of nine students.

The Scientific Work of the Plymouth Laboratory Staff.

As in last year's report the descriptions of the different investigations have been arranged so as to indicate their bearing on the general plan of work that is being undertaken by the staff. The investigations on the physical and chemical characters of the environment are first described, then those on the vegetable and animal plankton, which form the basis of the food supply of the sea. Researches on the ecology, physiology, and genetics of the invertebrates of the sea-floor which feed on the plankton and on each other are then described. These invertebrate animals constitute the food of the bottom-living fishes and lead naturally to an account of studies on the fishes themselves and the commercial fisheries.

Physics and Chemistry of the Environment.

Dr. Atkins and Dr. H. H. Poole have continued their work on the measurement of submarine illumination and an arrangement has been devised whereby the colour filters can be changed at various depths, so that alterations in intensity can be determined more nearly simultaneously for various colours. This method avoids errors introduced by a possible drift of the ship between the depth-series carried out with one colour filter after another. The photo-electric cells used in these investigations have now been standardised in terms of "mean noon sunlight," as defined by the Seventh International Congress of Photography, so that photo-electric measurements made at various places may be truly comparable. A laboratory study was also carried out upon the behaviour of the new type of photo cell described by Lange. This is used without a high-tension battery and is highly sensitive, but the current is not linearly proportional to the illumination over an extended range and there is a considerable temperature coefficient. Bearing such limitations in mind a cell of this type was mounted in a handy form of submarine photometer which was carried about under water by Mr. J. A. Kitching and Mr. Gilson while using the diving helmet in their survey of a submarine gully near Wembury. The photometers were calibrated against a vacuum photo-electric cell and precautions were taken to minimise the temperature effect.

Dr. Atkins has also shown that diphenylbenzidine is a serviceable reagent for estimating nitrate in sea-water. The reagent is readily prepared, the colour intense and stable to light. Since iodate reacts in a quantitatively similar manner it must be removed, if present.

Attention has also been given to the determination of the copper-content of sea-water on account of the recognition of the importance of this element in plant growth, in the utilisation of iron in the animal organism and as the stimulus, according to Prytherch, for the attachment of oyster larvæ. By means of electro-deposition and colorimetric estimation with sodium diethyl-dithiocarbamate sea-water was found to contain 10 mg. of copper per cubic metre. A more rapid method whereby the copper salt of the reagent is extracted with an organic solvent has also been used and a river water at low tide was found to contain 36 mg. as against 16 mg. per cubic metre at high tide.

The hydrographic records between Plymouth and Ushant, commenced in 1921, have been continued. These are published yearly in the *Rapport Atlantique* of the International Council for the Exploration of the Sea. They are also worked up by Mr. H. W. Harvey in conjunction with the surface data, collected for the Ministry and for this Association by cross-Channel steamers. Charts of the salinity distribution at the mouth of the Channel are drawn for each month. Reports on the major changes which have taken place are published in the Journal of the Association at intervals.

Much of Dr. L. H. N. Cooper's time has been spent in working up the mass of data on the minor constituents of sea-water obtained during 1931. Calculations of the phytoplankton crop in the Channel, based on seasonal changes in phosphate, nitrate, oxygen, and carbon dioxide and agreeing closely with one another, show that each square kilometre produces about 1,400 metric tons wet weight. The crop calculated from silicate data is less than one-tenth of this. Since silicate is seldom found completely exhausted and diatoms predominate in the phytoplankton, it is concluded that silicate takes part in the life-cycle several times in the course of the season. This is supported by the rapid re-solution of silicate after the spring outburst to give a summer maximum about July or August. The detailed results of this work are being published in the Journal of the Association. Work has been continued on certain of the nutrient salts. The summer maximum for silicate was again observed in 1932.

Plankton.

Mr. Harvey has continued an investigation concerning the influence of various factors upon the rate of assimilation and respiration by the diatom *Nitzschia closterium.* It was found that the addition of phosphate to a culture which had used up all or nearly all the available phosphorus, caused, in the dark, an increased rate of respiration and a division of cells.

In the light the addition of 10 mg. per cubic metre P_2O_5 brought about an increased fixation of some 115 mg. of carbon. The addition of either nitrate or ammonium to a culture which had used nearly all the available nitrogen caused a similar increase in the rate of growth in the light, the addition of 1 mg. of nitrogen bringing about an increased fixation of some 12 mg. of carbon. It was found that the addition of 1 mg. of iron per cubic metre, in the form of citrate, roughly doubled the rate of growth, and some evidence was obtained that iron is only available in ionic form, of which sea-water probably contains considerably less than one part in a thousand million. The addition of a sterilised extract of soil to a culture, enriched with nutrient salts, iron and silica, caused a material increase in rate of growth. If kept in the dark the addition caused a multiplication of the diatom cells. The presence of a " growth-promoting factor " in extract of soil, yeast, seaweed, and the diatom itself seems probable.

To a Nitzschia culture additions were made of recently distilled water and of an equal quantity of the same water which had been frozen and allowed to melt and attain room temperature. An increased growth was observed where the added water had previously been frozen. An increased growth was also observed where the culture fluid was partly frozen and then allowed to attain room temperature before inoculation with the diatoms. Further experiments on the apparent physiological action of trihydrone are being made.

Mr. F. S. Russell has made progress with his research on the biology of the plankton animal Sagitta. It has been possible to show that a number of broods are produced during the year the adults of which appear to grow to different sizes, those maturing in April and May being the largest. There are two species of Sagitta commonly occurring at Plymouth, *S. elegans* and *S. setosa ;* in their annual life-cycles the two species differ slightly. Both cease breeding for a period in the winter, but *S. setosa* continues to breed later than does *S. elegans*, an adult brood of the former appearing in October while the last brood of the latter to mature in the year appears in September. *S. setosa* would seem therefore to have one more brood than *S. elegans* during the twelve months. Both species show variation in the size to which adults of the different broods grow, but the range of this variation is greater in *S. elegans* than in *S. setosa*. These results have been published in the Journal, Vol. XVIII, No. 1. An examination of the Sagitta population over a number of years has shown that there has been a gradual change over from a population in 1930 in which *S. elegans* predominated to that of 1932 in which *S. setosa* predominates. An attempt has been made to find the actual relative abundance of the Sagitta throughout the year ; results based on oblique hauls with the 2-metre stramin ring-trawl appear to show a considerable dying down of the Sagitta stock during the winter months. Collections made with a stramin net fished very close to the bottom, however, show no such diminution and seem to suggest that the apparent diminution in the oblique catches may be due to the descent of the Sagitta to the deeper water-layers.

By piecing together the results of the above research and further results obtained from collections made in 1926 to study the vertical distribution, it has been possible to produce a preliminary picture showing the whole cycle of events in a Sagitta population throughout a year. Of especial interest in this is the rise of Sagitta into the upper highly illuminated layers in July, August, and September. This is a phenomenon that Mr. Russell has already shown for other plankton animals, notably the copepod *Calanus finmarchicus*. In its vertical distributions *S. setosa* always appears to live slightly higher in the water than does *S. elegans*. An account of the results of the above work is now in the press.

As an outcome of the researches on the pelagic young of teleostean fishes a record has been made of the occurrence of the fixed Chalimus stages of the Caligid parasitic copepods. It appears that two fishes, *Gadus merlangus* (whiting) and *Ammodytes lanceolatus* (sand-eel), are especially liable to parasitisation during their pelagic existence.

The weekly observations on the seasonal abundance of young fishes have been continued, and records are being kept of certain species of plankton animals, notably certain medusæ, that appear to characterise the plankton in different years. The last two years, 1931 and 1932, have been notable for the occurrence of Doliolids, and Mr. Russell has collaborated with Miss A. B. Hastings of the British Museum in a report of the occurrence of pelagic tunicates (Thaliacea) in the Plymouth area. In 1931 two species of Doliolum appeared, *D. nationalis* Borgert and *D. gegenbauri* Ulyanin, the latter being recorded for the first time at Plymouth. In the autumn of 1932, the salp, *Salpa fusiformis*, was unusually abundant. It is hoped to attempt to correlate the occurrence of these various plankton animals with the hydrographic conditions.

Mr. Russell has given a considerable amount of time to the working up of his report on the plankton of the Great Barrier Reef Expedition. This has necessitated reading widely into the reports of previous oceanographic expeditions and should give him a valuable insight into the general distribution of plankton organisms as a whole. He is now engaged on working up the vertical distribution collections made in collaboration with Dr. Atkins' light intensity observations in the summer of 1931.

Mr. G. M. Spooner has extended his experiments on reactions of plankton animals to light. A paper is being prepared embodying results which concern the relative importance of direction and change of intensity of light in determining the course of movement of photosensitive animals. The conflicting conclusions arrived at by previous investigators are satisfactorily explained. Attention is now being given to the influence of gravity on light reactions.

Dr. M. V. Lebour has continued her work on the life-histories of gastropods, many of which she has now worked out. The little-known veligers of the plankton, if studied alive, can be readily identified when once the connection between larval form and adult has been determined. Much has been done by keeping these planktonic veligers in plunger-jars until they metamorphosed. In order to rear them after this it is necessary to know the natural food of the adult, and this has been made a special part of the research, in many cases successful, in others difficult to ascertain. The failure to find the right food is apparently the reason for the failure to rear some of the metamorphosed larvæ which are still being studied. Papers on the life-histories of *Simnia patula*, *Limacina retroversa*, and the eggs and young of *Stilifer stylifer* and *Odostomia eulimoides* have appeared in the current number of the Association's Journal and there are now in the press papers on the British species of Trivia and on the life-histories of *Trivia arctica*, *Erato voluta*, *Cerithiopsis tubercularis*, *C. barleei*, *Triphora perversa*, *Turritella communis*, *Aporrhais pes-pelicani*, and *Philbertia gracilis*.

The work on larval Trivia has proved the existence of two British species (already established by other workers in the adult), *Trivia monacha* (Da Costa) and *Trivia arctica* (Montagu), the first with a more southerly distribution than the second and having a different breeding season, for whereas *T. monacha* breeds in summer, *T. arctica* breeds in winter. There is also a distinct difference in the larvæ of the two species. *T. arctica* has been reared in a plunger-jar from the late planktonic larva through metamorphosis until the adult state, being fed on compound ascidians. *Erato voluta,* closely related to Trivia, has a large helicoid Echinospira shell, the larva having certain peculiarities unlike any known mollusc. The adult Erato also feeds on compound ascidians. The late planktonic larva of this species metamorphosed in a plunger-jar. Six Echinospira larvæ have now been found in Plymouth, two of which belong to Trivia, two to Lamellaria, the others to Erato and Velutina, all belonging to the families Cypræidæ and Lamellariidæ which appear to have several features in common. On the other hand the larval Trivia are very unlike the other Cypræidæ known, including Simnia.

Further work on the life-histories of Velutina, several members of the Turridæ, Rissoidæ, and others is in progress and giving interesting results. The number of larval molluscs in the plankton is large and must be very important economically.

In continuation of her work on the larval Crustacea papers by Dr. Lebour on the life-history of *Spirontocaris cranchii*, and on the larvæ of the Plymouth Alpheidæ, have been published in the Proceedings of the Zoological Society. A female of *Dromia vulgaris* carrying eggs was sent to the Laboratory from the Cornish coast, and the eggs hatched out. The brilliant orange-red larvæ, which are very peculiar and quite unlike the zoeæ of ordinary crabs, were kept until they changed to the second larval stage but did not live longer.

As mentioned in the last Report of Council, Mr. D. P. Wilson had already a year ago completed his researches on the development and metamorphosis of the Mitraria larva of *Owenia fusiformis*. An account of the work has since been published in the Philosophical Transactions of the Royal Society. Continuing his studies on the development of larval Polychætes, he has succeeded in rearing several cultures of the larvæ of *Branchiomma vesiculosum*. Previous observations made on living larvæ have been confirmed, and a considerable quantity of material of all stages has been fixed and preserved. This material is at present being sectioned with a view to a detailed histological study, particularly of the curious metamorphosis.

Mr. Wilson has completed and published in the Journal an account of the development of *Nereis pelagica* based on a rearing made in 1927. He has also again reared *Notomastus latericeus* from the egg to an early bottom stage, confirming previous observations and making a few additions. A paper on the development of this species has been prepared for the Journal.

The work on the Mitraria larva having directed attention to the desirability of acquiring some knowledge of the development of Maldanids, a family whose embryology is as yet unknown, a special effort has been made with this end in view. A good patch of the worm *Caesicirrus neglectus* was, during the spring, located at Salcombe and has been visited at regular intervals ever since. Unfortunately these particular worms have not yet spawned, but it is hoped to obtain fertilisations as soon as they are ripe.

Invertebrates of the Sea Floor (Ecology, Physiology, Genetics).

The ecological survey of the Eddystone shell gravel which Mr. J. E. Smith commenced in January, 1931, was concluded in February of this year. The investigation included a study of the relations of the animals living in the gravel to their environment, and a discussion of the origin and nature of the gravel bottom in the immediate vicinity of the Eddystone reef. It is of interest that the shell constituent of the gravels consists only of the shells and tests of animals which normally live on the ground—evidence that the "shell gravel community" of animals is of a permanent and limited nature. A paper describing the survey and containing a discussion of the results has been published in the Journal of the Association.

During the summer months Mr. Smith has confined his attention to the collection of material for embryological work on Nemertines. Larvæ of *Cephalothrix rufifrons* (Johnstone) have been reared successfully to an advanced stage, and the early stages of segmentation have been studied both from living and preserved material. It is hoped ultimately to prepare for publication an account of the "direct" method of development of this Palæonemertine.

In July Mr. F. S. Russell paid a visit to Portsmouth to make a biological survey of H.M.S. *Champion* at the instigation of the Corrosion Committee of the Iron and Steel Institute. This was a preliminary examination to study the possible effects of the growth of marine organisms on corrosion of metal.

Dr. C. M. Yonge has made considerable progress with his investigations into the nature and permeability of crustacean chitin. A first paper on this subject on "The Chitin Lining the Foregut of Decapod Crustacea and the Function of the Tegumental Glands" was recently published in the Proceedings of the Royal Society. The integument was shown to consist of two distinct regions, a thin superficial cuticle and a much thicker, lamellated chitin. The former, as indicated in the Report for

1931, is formed by the tegumental glands which are everywhere abundant under all chitinous areas in the body of Crustacea (and also many other Arthropods), while the latter is secreted by the chitinogenous epithelium. The function of these glands has hitherto been a matter of speculation. The cuticle differs in chemical and physical properties from the chitin. Its true nature is still uncertain, but it is certainly *not* chitin. Experiments on the permeability of chitin are still proceeding (though approaching completion), and when they are published will establish definitely that the cuticle is of fundamental importance in controlling the permeability of the uncalcified chitin in the Crustacea and possibly in many other, or indeed all, Arthropoda.

In addition to the main objects of this research several interesting facts have been discovered. In the lobster, onwhich the great part of the work has been done, the formation of new chitin has been found to be preceded by the dissolution of the undermost layers of the old chitin. This is brought about by the agency of cells which migrate into it from the tissues and which apparently secrete a chitinase. It has also been possible to establish the true nature of the membranes which surround the eggs of Decapod Crustacea after they are attached to the pleopods of the female, and also the method of attachment, on both of which subjects there has, in the past, been much uncertainty. As the eggs pass down the oviduct they are covered with a thin layer of chitin and after extrusion they are wrapped round and secured to the pleopods by thin sheets of " cuticular " material secreted by the tegumental glands which are especially abundant in these appendages. The material used in the formation of nests by various Amphipoda and the cement secreted by the Cirripedia both appear to be of the same nature as the cuticle in the Decapoda. It is hoped to produce a paper shortly on the membranes and attachment of the eggs in the Decapods and, in the course of time, to follow up the preliminary investigations on the Amphipoda and Cirripedia.

Further progress has been made with the preparation and publication of work done during the Great Barrier Reef Expedition, and two papers, " The Relationship between Respiration in Corals and the Production of Oxygen by their Zooxanthellæ " (in collaboration with Mrs. Yonge and Dr. A. G. Nicholls) and " Notes on Feeding and Digestion on Pterocera and Vermetus with a Discussion on the Occurrence of the Crystalline Style in the Gastropoda," have been published in the Scientific Reports of the Expedition (British Museum Nat. Hist.). Short papers dealing with work done or observations made during the expedition have also been published in the Journal of the Malacological Society of London and in Natural History. A short account of the Crystalline Style in the Mollusca has been published in Science Progress. Some observations on planulation and early development in *Balanophyllia regia*, our only Eupsammiid coral, have been published in the Journal of the Association. Certain observations have also been made by Dr. Yonge on the iso-electric point of the mucus in ciliary feeders and the relation of the viscosity of the mucus to the hydrogen-ion concentration in various regions of the gut. This work will be incorporated in a forthcoming paper dealing with various aspects of digestion in ciliary feeders which differ from many other animals in that they feed *continuously*, which involves important correlations in the digestive processes.

The Mendelian work on *Gammarus* has been carried on by Mrs. Sexton with the assistance of Miss A. R. Clark, particular attention being directed during the past year to the question of the origin of recessive characters, especially as to how far they are present in the wild. A considerable amount of data has been collected which it is hoped will soon be ready for publication.

The paper, in collaboration with Mr. G. M. Spooner, referred to in last year's Report, dealing with the different stocks where variations in eye-pigmentation have occurred, has been published in the Journal, and has aroused considerable interest amongst those who are studying similar problems. In another paper Mrs. Sexton has given an account of a long series of degenerative changes grading from the perfect eye to the entire absence of one or both eyes. It is noteworthy that all these changes, which occurred in the same stock, took place within the short period of eight years.

Fish and Fisheries.

Mr. E. Ford followed the progress of the drift-net fishery for herrings during the winter of 1931–32. The commercial results were disappointing, the total quantity of fish landed and the total value both being the lowest since the season of 1921–22. The average weight of fish per landing was also low, comparing very unfavourably with the average of the past ten years, particularly in the case of the West-country motor-drifters. These results were not unexpected in view of the fact that there appears to have been a limited replenishment of the fish stocks by incoming recruits during recent years, so that the fishery has latterly been dependent upon a stock that is getting older and numerically weaker. The excellent fishery of 1929–30 was due in large measure to the presence of a high proportion of herrings of the successful year-class 1925, then in its fifth winter. The fisheries of 1930–31 and 1931–32 had also to rely for the most part on what still remained of this same year-class, since younger fishes of the broods of the years 1926, 1927, 1928, and 1929 were not entering the shoals to any noteworthy degree. Naturally, therefore, there was a marked fall in the average weight of fish per landing. The extent of this fall and the corresponding changes in the age composition of the catches are shown by the following figures :—

SEASON (Dec.–Jan.)	AVERAGE WEIGHT PER LANDING Steamer (cwt.)	Motor (cwt.)	AGE COMPOSITION OF CATCHES 3, 4 and 5 years °/₀	6 years °/₀	Older than 6 years °/₀
1929–30	39·1	42·5	55·9	15·4	28·8
1930–31	32·7	23·3	38·4	33·2	28·3
1931–32	17·6	9·2	31·0	21·3	47·7

In face of these results, the outlook for the immediate future of the fishery would appear to be serious, unless and until there are signs of an early renewal of the stocks by a big influx of young fish.

Fortunately, there are indications that the brood born during the winter of 1929-30 is about to enter the fishable stocks in good numbers, although final confirmation of the richness of the brood will not be forthcoming until the season of 1932–33 has opened. The examination of samples from an unusual run of herrings inshore during September and October of 1932 showed an exceptionally high proportion of the brood in question—a circumstance which is the basis of the hopes expressed above. Should the 1929–30 brood prove a rich one, the turn of the tide in the fisherman's favour may be expected next season, if not in this coming one.

In January last, Mr. Ford tried the experiment of forwarding developing herring eggs to the Laboratories at Cullercoats and Port Erin (Isle of Man) and to the Brighton Municipal Aquarium, in order that trials might be made to hatch out and rear the larvæ under the normal local conditions. The eggs were forwarded attached to the inside of glass jars (breffits) in which they had been fertilised, the travelling containers being ordinary hampers. They arrived safely at their destination and good hatching results were reported in each instance, although it was found impossible to rear the larvæ. The experiment was quite satisfactory in demonstrating that fertilised eggs can be sent considerable distances by the ordinary methods of transport, whereby the facilities afforded by other laboratories for rearing researches become available.

In addition to this new work, Mr. Ford has been preparing a comprehensive account of the different branches of herring research which have been conducted and reported on in this Journal in a series of separate papers entitled "Herring Investigations at Plymouth." This account which is nearing completion will serve the double purpose of co-ordinating the separate studies made, and of indicating the lines along which further investigation is needed.

An increase in the opportunity for members of the staff of the Laboratory to take part in the public work of the administration of the fisheries of

Devon and Cornwall has been afforded by the appointment of Mr. Ford as a member of the Devon Sea Fisheries Committee, and of the invitation of the Cornwall Committee for him to attend their meetings.

Mr. G. A. Steven has continued his researches on the rays and skates of the western area of the English Channel, and a report embodying many of the results so far obtained was published in the Association's Journal in May of this year. It has often been observed, and became evident again in these researches, that female fish considerably outnumber the males in ray landings. An effort has been made to ascertain whether or not this preponderance of females in the catches is due to excess of females in the ray population in the sea or to differential capture of the two sexes. Data have been collected which show that, in these waters at any rate, the young of the commonest species (*R. clavata*) are born with the sexes approximately equally represented. As growth proceeds and maturity is reached the sexes segregate to a greater or less extent, and the females, when in a gravid or "spawning" condition, form more compact shoals than do the males and therefore tend to be captured in greater numbers. What is true of *R. clavata* probably holds good also for all the other ray species. This fact has a direct practical bearing upon the commercial fishery for these species, which are now of considerable and steadily growing importance as national food fishes. For the maintenance of any animal stock the female is, from the numerical point of view, the more important sex. In the Raiidæ, therefore, the greatest drain of the fishery upon the fish population is falling upon its most vulnerable part. A report of this work has been prepared for publication in the Journal of the Association. During the year, as weather and tidal conditions permitted, determined efforts have been made to obtain ray eggs in a locality which is believed to be a "spawning" ground. In spite of every endeavour, no eggs have been found although large numbers of empty cases and not a few full ones are thrown up on adjacent shores during heavy autumn and winter storms. The liberation of marked rays, with a view to following their migrations and determining their growth-rate, has been continued and very satisfactory returns of recaptured specimens are being obtained. Most of the fish which have so far been marked have been in an immature condition and the recaptures have shown that they migrate but little, at any rate, until maturity is reached. Numerous fish have been recaptured in the exact place of liberation after periods of freedom varying from a few days up to a year or more. Growth is slow, apparently averaging about 4 cm. in width across the disc in one year in half-grown individuals (20 to 30 cm. disc width) of *Raia clavata*. Most of this growth takes place during the summer and autumn months. Many more data are required, however, on these points and are steadily being accumulated.

In order to disentangle the movements of immature and sexually mature fish, the state of maturity of all males which have been marked—as indicated by the size and condition of the claspers—has been recorded. But as there is no external evidence of the state of maturity in the female fish, this could not be done with them. Investigation has now revealed that certain changes in the size and condition of the cloaca and uterus, which take place at sexual maturity and which can be ascertained by digital examination of the live fish, form a ready means of separating mature from immature female individuals. This method will be applied in future marking experiments and should greatly add to the extent and value of the data acquired.

In continuation of his investigations on the food of Shags and Cormorants Mr. Steven endeavoured to obtain birds from certain harbours and sandy bays and estuaries around the Devon and Cornwall coasts. It is in such situations that fishermen claim most frequently to see these birds devouring flatfish, particularly during the winter season when they are driven in from their usual feeding-grounds by stress of weather. It has been found very difficult to obtain the birds from such places, but 2 Shags and 2 Cormorants were shot and secured in the sandy estuary of the river Erme on 2nd February, 1932. Although shot *inside* the estuary where young flatfish are numerous, these birds had obviously been feeding around the rocky shores *outside*, for the contents of each of the four stomachs was made up of rock-dwelling species. No evidence has yet been obtained, therefore, in support of the fishermen's claim that these birds make serious inroads on the flatfish population around these shores.

The preservation of fishing-nets has continued to receive attention from Dr. Atkins and a short report was made to the Advisory Committee on Vegetable Fibres concerning sisal, hemp, and Phormium fibre for trawl twines. Nets treated with copper resinate, dissolved in gasworks benzene or in solvent naphtha, have retained their colour and original strength intact for a year under the usual test conditions, under which the preservative comes off the surface at least, in the case of other reagents, unless bound with tar. The resinate costs one shilling per pound and gives a greenish coloured net, quite clean to handle and not greasy. A net treated by Dr. Olie's method and re-treated every four months has now remained in good condition for six years, the breaking strength of the twine averaging 16 lbs. as against 18 lbs. when new.

River Tees Survey.

Field work connected with the Biological and Chemical Survey of the River Tees Estuary was continued until the early summer of 1932. Methods of reducing the toxicity of cyanide-containing effluents were investigated and a large-scale experiment was successfully carried out with the help of Messrs. Dorman Long Ltd. at their Acklam works. Some 5000 gallons per hour were rendered innocuous by the addition of lime and spent pickle liquor, a local by-product containing ferrous iron. Unfortunately, considerations of expense did not allow the whole of the cyanide containing effluent discharged into the estuary to be treated during the period of the smolt run, and the projected investigation of the effect upon the mortality of smolt during their migration of rendering the cyanide innocuous had to be abandoned. The rest of the year has been devoted to finishing various parts of the experimental work and to writing a report of the survey. The investigation has been carried out at Middlesbrough under the direction of Dr. B. A. Southgate, with Mr. R. Bassindale as biological assistant, and Mr. H. W. Harvey has visited Middlesbrough from time to time and keeps in contact with the various investigations and with the administration by means of such visits and by correspondence.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association :—

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Finance.

The Council have again to express their thanks to the Development Commissioners for their continued support of the Plymouth Laboratory. They are grateful also for generous grants from the Fishmongers' Company (£600), the Royal Society (£50), the British Association (£50), the Physiological Society (£30, 1931), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol (£25), Birmingham (£15 15s.), Manchester (£10 10s.), Leeds (£21 ; 1931, 1932), Sheffield (£10), and the Imperial College of Science and Technology (£10).

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The following is the list of gentlemen proposed by the Council for election for the year 1933–34 :—

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List of Annual Subscriptions

Paid during the Year, 1st April, 1932, to 31st March, 1933.

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Prof. H. Munro Fox	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
Prof. F. E. Fritsch, F.R.S.	1	1	0
Prof. J. Stanley Gardiner, F.R.S.	1	1	0
John S. Gayner, Esq. (1931 and 1932)	2	2	0
Ghardaqa Marine Laboratory	1	1	0
R. D'O. Good, Esq.	1	1	0
Carried forward	97	13	0

	£	s.	d.
Brought forward	97	13	0
Prof. E. S. Goodrich, D.SC., F.R.S.	1	1	0
Alastair Graham, Esq.	1	1	0
David H. Graham, Esq.		14	11
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq.	1	1	0
Dr. A. M. H. Gray	1	1	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq.	1	1	0
Ian I. Hamilton, Esq.	1	1	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
J. E. Harris, Esq.	1	1	0
T. J. Hart, Esq. (1933 and 1934)	2	2	0
H. W. Harvey, Esq.	1	1	0
Prof. L. A. Harvey	1	1	0
G. T. D. Henderson, Esq.	1	1	0
C. C. Hentschel, Esq.	1	1	0
Prof. S. J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S. (1931 and 1932)	2	2	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
Prof. K. Hirasaka	1	1	0
Dr. E. G. Holmes	1	1	0
C. E. P. Hopkins, Esq.	1	1	0
N. H. Howes, Esq.	1	1	0
P. Hoyte, Esq. (1931 and 1932)	2	2	0
Hull University College	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., SC.D., F.R.S.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
J. A. Kitching, Esq.	1	1	0
Dr. E. M. Kreps (1932 and 1933)	2	2	0
Dr. G. Lapage	1	1	0
Prof. R. D. Laurie (1931 and 1932)	2	2	0
A. G. Lowndes, Esq.	1	1	0
C. E. Lucas, Esq.	1	1	0
Carried forward	143	10	11

	£	s.	d.
Brought forward	143	10	11
Adrian Lumley, Esq.	1	1	0
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Prof. D. L. Mackinnon, D.SC.	1	1	0
G. I. Mann, Esq.	1	1	0
B. J. Marples, Esq.	1	1	0
D. J. Matthews, Esq.	1	1	0
Capt. W. N. McClean	1	1	0
Milford Haven Trawler Owners & Fish Salesmen's Association, Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.SC., F.R.S.	1	1	0
F. W. Moorhouse, Esq.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerji	1	1	0
National Institute of Turkish Fisheries (balance)		1	0
National Museum of Wales, Cardiff	1	1	0
Miss G. L. Naylor	1	1	0
Dr. A. G. Nicholls	1	1	0
J. A. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Office Scientifique et Technique des Pêches Maritimes	1	1	0
Charles Oldham, Esq.	1	1	0
Prof. Yô Okada (1933 and 1934)	2	2	0
G. W. Olive, Esq.	1	1	0
R. Palmer, Esq.	1	1	0
The Hon. John H. Parker	1	1	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock & Buchan Ltd.	1	1	0
Pease Laboratories Incorporated	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
Carried forward	183	9	11

	£	s.	d.
Brought forward	183	9	11
W. Proctor, Esq.	1	1	0
W. P. Pycraft, Esq. (1930–1932)	3	3	0
Dr. A. Ramalho (1933 and 1934)	2	2	0
George Rayner, Esq.	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
E. A. Robins, Esq.	1	1	0
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
Dr. F. F. Schacht	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Lt.-Col. R. B. Seymour Sewell, C.I.E., I.M.S. (1932 and 1933)	2	2	0
Miss Lilian Sheldon	1	1	0
Prof. W. Rae Sherriffs, D.SC.	1	1	0
N. Smedley, Esq.	1	1	0
J. E. Smith, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	0
Mrs. N. S. Steven	1	1	0
E. J. Stream, Esq.	1	1	0
Eric J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Harold Thompson, Esq., D.SC.	1	1	0
Sir Herbert F. Thompson, Bart.	1	1	0
Torquay Natural History Society	1	1	0
Philip Ullyott, Esq.	1	1	0
A. Walton, Esq.	1	1	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
Carried forward	228	12	11

	£	s.	d.
Brought forward	228	12	11
Mrs. F. J. Weldon	1	1	0
Dr. K. B. Williamson	1	1	0
D. P. Wilson, Esq.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
Total	£237	0	11

List of Donations to the General Fund

For the Year, 1st April, 1932, to 31st March, 1933.

	£	s.	d.
Dr. S. Hatta	1	10	0
News Chronicle	5	5	0
Mrs. C. H. Roberts	2	1	0
Total	£8	16	0

List of Donations towards the Building Extension Fund

Paid during the Year 1st April, 1932, to 31st March, 1933.

	£	s.	d.
Trustees of Rockefeller Foundation	1,991	6	3
Sundry Donation	2	0	1
Total	£1,993	6	4

List of Composition Fees

Paid during the Year, 1st April, 1932, to 31st March, 1933.

	£	s.	d.
Prof. Dr. H. Boschma	15	15	0
Miss M. L. Rothschild	15	15	0
Total	£31	10	0

INCOME AND EXPENDITURE ACCOUNT

	£ s. d.	£ s. d.
To SALARIES, including Institutions Contribution to Superannuation		6,696 11 7
,, LABORATORY WAGES, including National Insurance and Institutions Contribution to Superannuation ..		2,100 5 9
,, DEPRECIATION OF LIBRARY		493 12 1
,, SCIENTIFIC PUBLICATIONS, *Less* SALES		631 2 11
,, UPKEEP OF LABORATORIES AND TANK ROOMS:		
Buildings and Machinery	308 15 8	
Electricity, Gas, Coal, Oil and Water	402 12 5	
Chemicals and Apparatus	342 15 5	
Rates, Taxes and Insurance	105 1 6	
Travelling	65 16 1	
Stationery, Postage, Telephone, Carriage and Sundries	327 11 3	
Specimens	180 10 0	
		1,733 2 4
,, MAINTENANCE AND HIRE OF BOATS:		
Wages, including Diet Allowance, National Insurance and Casual Labour	1,568 4 6	
Coal, Water, Oil, Petrol, etc.	217 3 9	
Maintenance and Repairs, with Nets, Gear and Apparatus	439 10 7	
Purchase of Material for Nets for Sale, excluding Labour	119 19 8	
Boat Hire and Collecting Expenses	18 17 0	
Insurance	300 13 0	
		2,664 8 6
,, TRANSFER TO DEPRECIATION RESERVE ACCOUNT ..		263 3 9
,, BALANCE, BEING SURPLUS FOR THE YEAR		195 4 3
		£14,777 11 2

BALANCE SHEET

		£ s. d.	£ s. d.
SUNDRY CREDITORS:			
On Open Account		145 1 3	
Wages accrued		53 1 3	
			198 2 6
BUILDING FUND:			
As at 31st March, 1932		285 8 7	
Add: Rockefeller Foundation Grant		1,849 17 8	
do. for Apparatus		141 8 7	
Sundry Donations		2 0 1	
		2,278 14 11	
Less: Expenditure:			
Library and Laboratory ..	287 8 8		
Rockefeller Laboratories ..	1,849 17 8		
Rockefeller Apparatus ..	141 8 7		
		2,278 14 11	– – –
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:			
As at 31st March, 1932		500 0 0	
Add: Transfer from Income and Expenditure Account		263 3 9	
			763 3 9
BANK OVERDRAFT:			
Coutts & Co. (Secured by Deposit of Investments) ..			173 2 7
SURPLUS:			
As at 31st March, 1932		5,625 1 9	
Add: Composition Fees		31 10 0	
Surplus for the year as per Income and Expenditure Account		195 4 3	
			5,851 16 0
			£6,986 4 10

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Associa
erection of Buildings on Land held on lease from the War Department is excluded. Subject
and correct view of the state of the Association's affairs, according to the best of our informati

34 *and* 35 *Bedford Street,*
Plymouth. *8th April*, 1933.

(Signed) R. A. FISHER } *Members of*
GUY WOOD } *Council.*

ION OF THE UNITED KINGDOM

YEAR ENDED 31st MARCH, 1933.

	£ s. d.	£ s. d.
By Grants :		
Ministry of Agriculture and Fisheries, Grant from Development Fund	11,258 6 10	
Fishmongers' Company	600 0 0	
British Association	50 0 0	
Royal Society	50 0 0	
Physiological Association (2 years)	60 0 0	
		12,018 6 10
,, Subscriptions		237 0 11
,, Donations		8 16 0
,, Sales :		
Specimens	1,173 16 5	
Fish (*less* expenses)	65 14 6	
Nets, Gear and Hydrographical Apparatus	253 9 1	
		1,493 0 0
,, Table Rent		454 3 9
,, Tank Room Receipts		497 17 6
,, Interest on Investments and Bank Deposits ..		40 19 1
,, Sale of Dr. M. V. Lebour's Book	4 15 10	
,, Sale of "Marine Fauna of Plymouth"	12 4 0	
		16 19 10
,, Refund of Income Tax		10 7 3
		£14,777 11 2

31st MARCH, 1933.

	£ s. d.	£ s. d.
Boats and Equipment, as per Valuation as estimated by the Director at 31st March, 1931 :		
S.S. *Salpa*	2,000 0 0	
Motor-boat	150 0 0	
Nets, Gear and General Equipment	27 0 0	
		2,177 0 0
Laboratory Apparatus, Engines and Pumps :		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost		
As at 31st March, 1932	540 12 8	
Additions during the year	39 10 2	
		580 2 10
Library :		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost less Depreciation		
As at March, 1932	1,985 11 5	
Additions during the year	590 1 10	
	2,575 13 3	
Less : Depreciation	493 12 1	
		2,082 1 2
Stock of Specimens, Chemicals and Journals as estimated by the Director		350 0 0
Sundry Debtors		133 8 1
Prepayments		98 7 6
General Fund Investments, at Market Value as at 31st March, 1931 :		
£410 14s. 8d. New Zealand 4% 1943/63	344 15 0	
£352 2s. 3d. Local Loans 3%	232 7 10	
(Market Value at Date—£734 18s. 6d.)		
		577 2 10
Depreciation Fund Investments at Cost		
£590 6s. 0d. Local Loans 3%	506 10 9	
£263 10s. 1d. Conversion Loan 3%	256 13 0	
(Market Value at Date—£783 0s. 2d.)		
		763 3 9
Composition Fee Fund Investments at Cost :		
£18 8s. 6d. Local Loans 3%	15 15 0	
£32 9s. 6d. Conversion Loan 3%	31 10 0	
(Market Value at Date—£48 6s. 11d.)		
		47 5 0
Cash at Bank and in Hand :		
Lloyds Bank Limited	161 10 3	
Cash in Hand	16 3 5	
		177 13 8
		£6,986 4 10

ll have obtained all the information and explanations we have required. Capital expenditure on remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true he explanations given to us and as shown by the books of the Association.

(Signed) Price, Waterhouse & Co.

Marine Biological Association of the United Kingdom.

LIST

OF

Governors, Founders, and Members.

AUGUST, 1933.

* Member of Council. † Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea.

C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual Subscription.

I.—Governors.

The British Association for the Advancement of Science, *Burlington House, W.* 1	£1,090
The University of Oxford	£920
The University of Cambridge	£1,182 10*s*.
The Worshipful Company of Clothworkers, 41 *Mincing Lane, E.C.* 3	£625
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4	£22,755
The Zoological Society of London, *Regent's Park, N.W.* 8	£505
The Royal Society, *Burlington House, Piccadilly, W.* 1	£1,065
Bayly, Robert (the late)	£600
Bayly, John (the late)	£600
Thomasson, J. P. (the late)	£970
*G. P. Bidder, Esq., Sc.D., *Cavendish Corner, Cambridge*	£3,508
*E. T. Browne, Esq., B.A., *Anglefield, Berkhamsted*	£2,045
‡*The Lord Moyne, P.C., D.S.O., 10 *Grosvenor Place, London, S.W.* 1	£1,000

II.—Founders.

1884	The Corporation of the City of London	£210
1884	The Worshipful Company of Mercers, *Mercers' Hall, Cheapside, E.C.* 2	£341 5*s.*
1884	The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, E.C.*	£100
1884	The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1	£152 10*s.*
1884	Bulteel, Thos. (the late)	£100
1884	Burdett-Coutts, W. L. A. Bartlett (the late)	£100
1884	Crisp, Sir Frank, Bart. (the late)	£100
1884	Daubeny, Captain Giles A. (the late)	£100
1884	Eddy, J. Ray (the late)	£100
1884	Gassiott, John P. (the late)	£100
1884	Lankester, Sir E. Ray, K.C.B., F.R.S. (the late)	£101
1884	The Rt. Hon. Lord Masham (the late)	£100
1884	Moseley, Prof. H. N., F.R.S. (the late)	£100
1884	The Rt. Hon. Lord Avebury, F.R.S. (the late)	£100
1884	Poulton, Prof. Edward B., M.A., F.R.S., *Wykeham House, Oxford*	£110
1884	Romanes, G. J., LL.D., F.R.S. (the late)	£100
1884	Worthington, James (the late)	£100
1885	Derby, the late Earl of	£100
1887	Weldon, Prof. W. F. R., F.R.S. (the late)	£100
1888	Bury, Henry, M.A., *The Gate House,* 17 *Alumdale Road, Bournemouth West*	£100
1888	The Worshipful Company of Drapers, *Drapers' Hall, E.C.* 2	£315
1889	The Worshipful Company of Grocers, *Poultry, E.C.* 2	£120
1889	Thompson, Sir Henry, Bart. (the late)	£110
1889	Revelstoke, The late Lord	£100
1890	Riches, T. H., B.A., *Kitwells, Shenley, Herts.*	£430
1892	Browne, Mrs. E. T., *Anglefield, Berkhamsted, Herts*	£100
*1902	Gurney, Robert, D.Sc., *Bayworth Corner, Boars Hill, Oxford*	£109 1*s.*
1904	Shaw, J., K.C., *Adderbury House, Banbury, Oxfordshire*	£113
1909	Harding, Colonel W. (the late)	£115 15*s.*
1910	Murray, Sir John, K.C.B., F.R.S. (the late)	£100
1912	Swithinbank, H., F.R.S.E., F.R.G.S. (the late)	£100
1913	Shearer, Dr. Cresswell, F.R.S., *Anatomy School, Cambridge*	£100
1913	Heron-Allen, E., F.R.S., F.L.S., F.R.M.S., F.G.S., *Large Acres, Selsey Bill, Sussex*	£125 15*s.*
†*1918	Evans, George, 1 *Wood St., London, E.C.* 2	£103
1920	McClean, Capt. W. N., 1 *Onslow Gardens, S.W.* 7	£100
1920	Buckland of Bwlch, The Right Hon. Lord (the late)	£105
1920	Llewellyn, Sir D. R., *The Court, St. Fagan's, Glamorgan*	£105
1921	Harmer, F. W. (the late)	£100

1898	Worth, R. H., 42 *George Street, Plymouth*	£120 15*s.*
1924	The MacFisheries, Ltd., 125 *Lower Thames Street, E.C.* 3	£100
1924	Murray, Lady	£100
1925	The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1	£100
1927	Bidder, Miss Anna, *Cavendish Corner, Cambridge*	£105
†1899	Iveagh, The Rt. Hon. the Earl of, 11 *St. James's Square, S.W.* 1	£145 15*s.*

III.—Members.

1900	Aders, Dr. W. M., O.B.E.	£5 and Ann.
1928	Aikawa, Hiroaki, *Imperial Fisheries Experimental Station, Fugakawa, Tokyo, Japan*	Ann.
*1895	Allen, E. J., D.Sc., LL.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth*	£25 10*s.* and Ann.
1925	Amemiya, Dr. Ikusaku, *University of Tokyo* (*Agriculture and Fisheries Department*), *Tokyo, Japan*	Ann.
1927	Amirthalingam, C., Ph.D., *Indian Museum, Calcutta, India*	£1 1*s.* and Ann.
1932	Aquario Vasco da Gama (Director, Dr. A. Ramalho), *Dafundo, Lisbon, Portugal*	Ann.
1933	Arbuthnot, J. W., *Trinity College, Cambridge*	Ann.
1910	Ashworth, Prof. J. H., D.Sc., F.R.S., *Zoology Department, The University, West Mains Road, Edinburgh*	£2 2s. and Ann.
†1911	Astor, The Right Hon. the Viscount, 4 *St. James's Square, London, S.W.* 1	£10 and *C.*
1929	Atkins, Miss D., *Oak Cottage, Chichele Rd., Oxted, Surrey*	£1 1*s.* and Ann.
1910	Atkinson, G. T., *Fisheries Office, Esplanade, Lowestoft, Suffolk*	£1 1s. and *C.*

1920	Baker, J. R., *New College, Oxford*, and *The Dell, Malvern Wells*	£1 and *C.*
*1928	Barcroft, Prof. J., F.R.S., *Glenveagh, Grange Road, Cambridge*	£2 and Ann.
1923	Barnard, T. T., *Duncote Hall, Towcester*	£11
1930	Barrett, W. H., *Brickfields, Harrow, Middlesex*	Ann.
1932	Bateman, J. B., Ph.D., *Kaiser Wilhelm Institut, Heidelberg, Germany*	Ann.
1929	Bayliss, L. E., Ph.D., *The Laboratory, Citadel Hill, Plymouth*	£13 3s. and *C.*
1885	Beck, Conrad, C.B.E., 34 *Upper Addison Gardens, London, W.* 14	*C.*

†1907 Bedford, His Grace the Duke of, K.G., *Endsleigh, Tavistock* £20 and *C.*

1928 Beer, G. R. de, 6 *High Street, New Headington, Oxford* .... Ann.

1926 Bělehrádek, J., M.D., *Docent of General Biology, Masaryk University (Medical Faculty), Brno, Czechoslovakia*.................. Ann.

1925 Berrill, N. J., D.Sc., *McGill University, Montreal, Canada* ...... Ann.

1903 Bidder, Colonel H. F., *Ravensbury Manor, Mitcham, Surrey*...... Ann.

1925 Birkbeck College, *Bream's Buildings, Fetter Lane, London, E.C.* 4 Ann.

1931 Birtwistle, W., o/c. *Fisheries Department, P.O. Box* 744, *Singapore* .... Ann.

1930 Blaschko, Dr. H., *Kaiser Wilhelm Institut, Heidelberg, Germany* Ann.

1910 Bloomer, H. H., "*Longdown,*" *Sunnydale Road, Swanage, Dorset* .... Ann.

1921 Blundell, H. S. Moss, *Ministry of Agriculture and Fisheries,* 43 *Parliament Street, London, S.W.* 1 .... Ann.

1922 Blundell, Mrs. H. Moss, *Callipers Hall, Chipperfield, King's Langley, Herts*... Ann.

1930 Bogorov, Dr. B. G., *State Oceanographical Institute, Herzen str.* 6, *Moscow, U.S.S.R.* .... Ann.

1932 Bolitho, Capt. R. J. B., *Ponsandane, Penzance* .... Ann.

†1910 Borley, J. O., O.B.E., M.A., 5 *Queen Anne's Chambers, Dean Farrar Street, S.W.* 1.................................. £1 1*s.* and Ann.

1928 Borowik, Dr. J., *Director of the Baltic Institute,* c/o. *Marine School, Gdynia, Poland* .... £2 2*s.* and Ann.

1918 Borradaile, L. A., Sc.D., *Selwyn College, Cambridge* £2 2*s.* and Ann.

1933 Boschma, Prof. Dr. H., *Zoölogisch Laboratorium, Leiden, Holland* .... *C.*

1931 Boulenger, Prof. C. L., *Bedford College for Women, Regent's Park, London, N.W.* 8 .... Ann.

1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W.* 8.. Ann.

1898 Bowles, Col. Sir Henry, Bart., *Forty Hall, Enfield, Middlesex* £8 4*s.* 8d. and Ann.

1924 Bowman, A., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen* .... £1 1s. and Ann.

1928 Boycott, Prof. A. E., F.R.S., 17 *Loom Lane, Radlett, Herts.* £1 and Ann.

1910 Bradford, Sir J. Rose, K.C.M.G., M.D., D.Sc., F.R.S., 8 *Manchester Square, London, W.* 1.. Ann.

1926 Branfoot, J. M., *Oundle School, Oundle, Peterborough, Northants* Ann.

1902 Brighton Public Library (Henry D. Roberts, Chief Librarian)... Ann.

1924 Brightwell, L. R., *White Cottage, Chalk Lane, Horsham, Sussex* Ann.

1933 Bristol University, Department of Zoology.......................... Ann.

1886 Brooksbank, Mrs. Mary, *Compton House, Lindfield, Sussex* ...... *C.*

1884 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*... £45 and *C.*

1929 Brown, R., *Seale Hayne College, Newton Abbot, Devon*............ Ann.
1924 Brown, W. Hargreaves, c/o *Messrs. Brown, Shipley and Co., Founder's Court, Lothbury, E.C.* 2 .... £10 10*s.*
1928 Brown, Miss E. M., 53 *Pepys Road, Wimbledon, S.W.* 20 £1 and Ann.
1925 Bull, Herbert O., Ph.D., *Dove Marine Laboratory, Cullercoats, Northumberland* .... Ann.
1920 Burne, R. H., M.A., F.R.S., *Royal College of Surgeons, Lincoln's Inn Fields, London, W.C.* 2 .... £15 10*s.* and Ann.
1930 Burton, M., *British Museum (Natural History), Cromwell Rd., London, S.W.* 7 .... Ann.
1925 Bush, S. Frank.. Ann.
1926 Butler, R. R., *Aston Technical College, Aston, Birmingham* £1 1 and Ann.
1897 Byrne, L. W., 7 *New Square, Lincoln's Inn, London, W.C.* 2 £7 7*s.* and Ann.

*1920 Cannon, Prof. H. Graham, Sc.D., *Victoria University, Manchester* .... £2 2s. and Ann.
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1931 Cattell, Dr. McKeen, *Cornell University Medical College*, 477 *First Avenue, New York City, U.S.A.* .... *C.*
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*1931 Graham, Michael, *Fisheries Laboratory, Lowestoft, Suffolk* ...... Ann.
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1929 Mukerjii, Dr. J., *Zoological Laboratory, University College of Science,* 35 *Ballygunge Circular Road, Calcutta* .... Ann.
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*1928 Norman, J. R., *Natural History Museum, Cromwell Road, S.W.* 7 Ann.

1931 Office Scientifique & Technique des Pêches Maritimes, *Laboratoire de Lorient, Port de Lorient-Keroman, France*.......... Ann.

1933 Okada, Prof. Yaichiro, *Zoological Institute, Normal College, Koishikawa, Tokyo, Japan* .... Ann.
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1931	Rothschild, Victor, 4 *Palace Green, London, W.* 8	Ann.
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1884	Sclater, W. L., 10 *Sloane Court, London, S.W.* 1	Ann.
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1921	Scott, Peter, *Leinster Corner, Lancaster Gate, London, W.* 2	*C.*
1928	Sen, B., *Vivekananda Laboratory, Baghbazar, Calcutta, India*	Ann.
1922	Sewell, Lieut.-Col. R. B. Seymour, Sc.D., C.I.E., *Zoology Laboratory, The Museums, Cambridge*	Ann.
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OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

Professor Huxley, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the Duke of Argyll, Sir Lyon Playfair, Lord Avebury, Sir Joseph Hooker, Dr. Carpenter, Dr. Günther, Lord Dalhousie, Professor Moseley, Mr. Romanes, and Sir E. Ray Lankester.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000 and from that time until 1933 a sum of over £16,000 has been spent on additional buildings. Throughout this period investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the maintenance of a research steamer and other collecting boats, and the salaries of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

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A Short Investigation into the Habits, Abundance, and Species of Seals on the North Cornwall Coast.

By

G. A. Steven, B.Sc., F.R.S.E.,
Assistant Naturalist at the Plymouth Laboratory.

(Report to the Ministry of Agriculture and Fisheries—30th December, 1932.)

With Charts I–III.

I. INTRODUCTORY.

DURING recent years Cornish fishermen have been complaining bitterly of the damage wrought by seals amongst their several fisheries. The fishing communities in the Lizard and Land's End areas claim that these animals rob their trammel nets and also that they not infrequently disperse shoals of mullet, a single haul of which in favourable circumstances will often yield a large sum of money—enough to ensure for the inhabitants of an entire fishing village a good winter's livelihood.

The most serious charges against the seals have been received, however, from the North Cornwall coast. The fishing communities situated along that shore complain that the seals frequent the herring fishing grounds and remove from the drift nets many of the herrings which have become enmeshed therein. The loss of fish thus entailed does not seriously embarrass these men in a good fishing season. But when fish are scarce and the catches small it is claimed that the activities of the seals constitute a grave menace to their already precarious livelihood.

According to reports sent in by the fishermen, the Grey Seal is the chief offender in this respect.

At the request of the Ministry of Agriculture and Fisheries, the Director of the Plymouth Laboratory of the Marine Biological Association instructed the writer to visit some of the Cornish fishing ports during the present herring season and find out by direct observation* with the

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* It must here be pointed out that herring drifting takes place mainly during the hours of darkness. The fishing vessels leave harbour in time to reach the fishing grounds at or just before sundown. Opportunity for the clear observation of seals and their activities amongst the boats and by the fishing nets is restricted therefore to the hours of failing daylight when the boats are proceeding to the grounds or while they are returning to harbour after daybreak—if they remain out until that time. After darkness falls, unless in very bright moonlight, a seal can be seen only if it should come within the circle of light cast upon the water by the boat's fishing lamps.

NATIONAL ACADEMY OF SCIENCES
JUN 19 1934
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fishing fleets to what extent these complaints are justified, and at the same time to determine—if possible—whether Grey Seals are numerous in the area.

The observations made and the results obtained form the substance of this report.

II. Places Selected.

It was ascertained from the Cornwall Sea Fisheries Committee that serious complaints concerning the depredations of seals are most frequently received from the fishermen of St. Ives, Port Isaac, and Padstow. Arrangements were accordingly made to go to sea with one of the herring drifters operating from each of those places. Owing to the success which attended the work at the two first-named ports, Padstow was not visited. At the special request of the Chairman of the Cornwall Sea Fisheries Committee, however, a visit was paid to Sennen Cove, near Land's End.

It was found that the Sennen fishermen, having heard that an investigation was in progress, wished merely to make verbal testimony to the damage wrought by seals amongst their several fisheries. It is from this village, for example, that the complaints regarding trammel nets and mullet shoals mainly have emanated. As no trammels were in use at the time of the visit and no mullet shoals in the vicinity, more direct evidence* of the activities of the seals in that locality could not be obtained. Two attempts were made, however, to visit the Longships Rocks where, the fishermen stated, seals may frequently be seen in considerable numbers. Although the sea was calm in Sennen Bay it was found to be too rough outside to approach the Longships on both the occasions on which an attempt was made.

III. The Seal Menace.

As will be seen from the Appendix (p. 496) subjoined to this report, three trips were made to the herring grounds in the vicinity of St. Ives in a herring drifter normally employed in fishing. While thus accompanying the herring fleet, five seals were sighted.

None were observed during the first night at sea in the vicinity of Cligga Head and Perran Beach (see Chart II, p. 499). On the second evening three seals were passed on the way to the fishing grounds off Zennor Head, only about 5 miles distant from the harbour (see Chart I, p. 497). Another seal was later observed about 150 yards away from the boat while the nets were being "shot." On the following morning in the vicinity of Pen Enys Point, a very large seal was seen within the circle of light cast by the boat's fishing lamps. It appeared to have come from the direction of the land, but just as it was sighted it turned towards the near net along the side of which, swimming rapidly, it disappeared outwards in the darkness.

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* Which was the object of this investigation.

During the single night spent at sea in Port Isaac Bay eight seals were sighted (see Appendix, p. 500). Before reaching the fishing ground only 2 miles distant from the harbour, three seals were passed. One of these appeared and disappeared several times by the side of another boat's train of nets. A fourth seal subsequently appeared close by the cork-rope supporting our own near net and a fifth about half-way along it. The latter disappeared in the gathering darkness following the line of the cork-rope. A sixth seal made its appearance a short distance to seaward of the boat. While the nets were being hauled, one seal remained for a considerable time close behind the vessel's stern, apparently following in her wake as she moved slowly along. Still another made its appearance near the outer edge of the illuminated area around the boat hard by the side of the net which was then being hauled in. Several times this seal disappeared only to reappear in the same relative position.

These are all the observations which were made actually with the fishing fleets at sea. More time spent with them would have produced only a needless repetition of the same kind of data without adding in any way to the value of those already obtained*—which show very clearly that seals are numerous on the North Cornwall inshore herring fishing grounds and that *they do haunt the nets of the herring drifters.*

IV. Abundance of Seals.

In addition to keeping a look-out for seals on the fishing grounds, two special exploratory cruises were made in search of them. From St. Ives, on Monday, 21st November, a cruise was made along the shore, eastward from the harbour, as far as Basset Island, where seals are reported to be very numerous (see Appendix and Chart III, p. 500). Only four seals were sighted during the entire trip which extended to about 18 miles† and occupied approximately three hours. This may have been due to the fact that a heavy ground swell was running, and it is much more difficult to catch sight of a dark object in the water when its surface is very broken and uneven than when it is calm and smooth. It is of particular interest to note, therefore, that on Monday, 5th December, over 100 seals of all sizes were reported to have been seen lying on a sand beach at the foot of a cliff on the mainland immediately opposite Basset Island. This beach is inaccessible except by sea, and then only in calm weather.

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* See also p. 494 of this report.

† On the return journey a "wide circle" was made to seaward as it was thought that the stormy sea might have caused the seals to forsake the immediate vicinity of the rocks.

On Wednesday, 7th December, a visit was paid to some caves—locally known as " seal holes "—about two miles west from Boscastle, in which seals were said by the Port Isaac fishermen to make their homes and to breed. All but one of these caves are inaccessible except by sea, and it was just about high water when they were reached by boat from Port Isaac. The caves are four in number,* situated close together some hundreds of yards north of the Gull Rock (also known as Beeny Island). All have relatively very small openings in the face of high rocks. One of the openings was too small for a boat to enter it, but the cave could be seen to " open out " inside to unascertainable dimensions. A second cave had its opening completely submerged so that it became visible only when the water subsided between successive waves. The two others it was found possible—though difficult because of the swell—to enter.

The northernmost cave was penetrated for a distance of about 100 yards. Here further progress was checked by the complete darkness ahead. Even at this distance from its mouth the water in the cave was over 8 feet deep and it was sufficiently disturbed to make an unseen rock a dangerous obstacle in the way of the heaving dinghy. It was possible to make out, however, that at this point the tunnel-like neck of the cave expanded into a vast cavern in which the troubled waters made loud and fearsome noises. No seals could, of course, be discerned in the darkness, and, unfortunately, no lantern was available.

On arrival at these caves not a single seal was to be seen. On emerging again from the first one entered, and in which a commotion had been made by beating empty petrol cans and buckets, a large number of seals were found to have made their appearance. They were in a state of much activity and excitement, diving and reappearing with great frequency, but always remaining close to the base of the cliffs.

The second accessible cave was then entered but its roof was so low that the rise and fall of the surging sea made it dangerous to venture far for fear that the dinghy might be crushed against the rocks above and swamped. On coming out, still more seals were in evidence. Loud noises were made at the mouths of the other two caves, which could not be entered because of the conditions prevailing, in order to cause the seals to come out if any were inside.

Because of the rough sea a more thorough exploration of the caves was impossible. There can be but little doubt, however, that the seals which made their appearance in the sea at their mouths had emerged from them. Having been disturbed, they came out—as was to be expected—under the water, which was then sufficiently deep in all the caves for them to emerge unseen. One large seal was observed, however, swimming rapidly out of one of the caves on the surface of the sea, and two others on being approached disappeared into the submerged opening already mentioned.

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* There are other " seal holes " in this vicinity which were not visited.

At the end of 1½ hours in the vicinity a great many seals had appeared. Their number could not be ascertained with any degree of accuracy as they were in a state of too much activity. Nevertheless, six or seven heads were generally to be seen on the surface at one time, and in one instance no less than nine different seals were in view near the mouth of one cave at the same moment.

It can safely be stated, therefore, that *in addition to the numerous seals scattered over the various herring grounds at this time, there is at least one seal colony of considerable size in the vicinity of Boscastle*, on the North Cornwall coast. It is probable that there are other such colonies in the same locality and at other places along that county's northern shore. Little evidence has as yet been collected which will either support or contradict the view that these seal resorts may also be breeding places. It may be significant, however, that among the seals which were seen near Boscastle there were several very young individuals* present among others which were obviously old adults.

V. Species of Seals.

It is very difficult, while actually at sea, to distinguish *with certainty* the Brown Seal (*Phoca vitulina*) from the Grey Seal (*Halichœrus grypus*) unless a clear view of the animal can be obtained at very close range. When, in the course of this investigation, a seal was sighted, but in such conditions that identification was impossible, the animal was recorded simply as "SEAL." When a better view was obtained and the species could be determined with reasonable certainty, this additional information is added to the log (see Appendix to this report). It is clearly to be understood, however, that these tentative identifications of live animals must be considered fallible and by no means final.

It will be seen in the Appendix that for only five animals are such identifications given. Of these, one is recorded as a Brown Seal and four as Grey Seals. In addition, *all those seen near Boscastle appeared to be Grey Seals.* If these identifications are correct, *it would appear that the Grey Seal* (*Halichœrus grypus*) *is much the more common of these two species along the shores of Cornwall.* This conclusion is supported by the fact that the seal which was washed up dead on the beach at Porthminster, near St. Ives, was found on examination to be *Halichœrus grypus*. Two other dead seals were later washed ashore near St. Ives both of which were also *Halichœrus grypus*.

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* See also p. 494.

VI. Discussion of Results.

Although there can be no doubt that seals do haunt the nets of the herring fishermen along the North Cornwall coast, definite proof that they actually rob the nets could not be obtained. Nor will this information readily be secured simply by making observation from a herring drifter normally employed. For complete elucidation of this problem a separately-conducted investigation would be required and special methods adopted or devised. If fish are removed from the nets by seals, this is done under water where—except in exceptional circumstances—their actions cannot be observed. An investigator might, therefore, spend a whole season, or even many seasons, in an ordinary fishing boat without adding materially to the information contained in this report. He might not for a long time be fortunate enough even to catch sight of a seal rising to the surface with a fish in its mouth*—an observation which the Cornish fishermen claim occasionally to make and to which they attach very great significance. For the purpose of their argument in favour of the destructive activities of seals they ignore the fact that some herrings are always lost from herring nets before they can be hauled inboard. In the absence of definite proof one way or the other two possibilities must, therefore, be kept in mind : (1) that the seals are attracted to the nets by these "dropped" herrings (which sink to the sea bottom where, in shallow water, they form an easily available food supply) ; and (2) that the seals definitely rob the nets.

One thing, however, is certain. Very seldom indeed does a seal become entangled in a drift net or is it responsible for causing damage to it in any other manner whatsoever. This statement can be made with complete confidence. It is backed by the present observer's knowledge of seals in other localities and the Cornish fishermen acknowledge that it holds good also in their waters.

As regards the species of seal at present found on the Cornish fishing grounds, it is interesting to note that the Grey Seal (*Halichœrus grypus*) was recorded from the North Cornwall coast as long ago as 1883. In that year Sir E. Ray Lankester found a newly born Grey Seal on the shore at Pentargon Cove, near Boscastle, and had it conveyed to the Zoological Gardens, Regent's Park, but it soon died in captivity. Lankester believed, however, that the Grey Seal was extremely rare in Cornwall and that the Brown Seal was the more abundant species (*Diversions of a Naturalist*, 1915 ; p. 32 *et seq.*). The very opposite appears to be true at the present time. This fact is of particular importance in view of the statement made by Hjort and Knipowitsch (*Rapports et Procès-Verbaux*, Vol. VIII,

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* On one occasion, many years ago, the writer himself caught sight of a seal rising to the surface of the water with a fish (not a herring) in its mouth.

1907 ; p. 114) concerning the Grey Seal. According to these authors "fish form its main food and it is in the Baltic, probably, the most harmful of the three species occurring there." The stomachs of three individuals of this species from the vicinity of St. Ives have been examined with the following results.

Date Examined.	Locality where found.	Stomach Contents.
21/11/32	Porthminster (St. Ives).	Herring Bones and traces of Herring Spawn.
28/11/32	St. Ives.	Beak of Cuttlefish (Sepia sp.).
13/12/32	St. Ives.	Clupeoid remains.

These data from Cornwall are too scanty as yet to justify any definite conclusion being drawn from them other than that *fish* (*herrings*) *do to some extent enter into the diet of the Grey Seal in those waters.*

Little is known, and the present writer has been able to find out nothing, concerning the breeding places (if any) of seals in Cornwall. Lankester (*op. cit.*, p. 33) was of opinion that whilst "the Brown Seal produces its young most usually in caves or rock-shelters, the Great Grey Seal chooses a remote sand island or deserted piece of open shore for its nursery." Sufficient evidence is not available to settle the question of whether or not this statement is justified—at any rate as far as the Cornish coast is concerned. Unless the present writer be in error concerning the seal colony at Boscastle, *Halichœrus grypus* is an inhabitant of caves in that locality. It probably also breeds there. (See also p. 492 of this report.)

The presence or absence of a cave-dwelling habit will have a marked effect upon the results which will attend any effort to reduce the numbers of seals. If a reward be offered for every head produced few seals will meet death by shooting, as only a small percentage of the animals so killed are recoverable. Two other methods will probably be extensively employed : (1) that of entering the caves in which seals are known to congregate and killing as many as possible with heavy cudgels ; and (2) that of driving them out of such caves to be entangled in strong nets previously fixed across the cave openings. Both these methods of hunting were formerly practised in Cornwall when the killing of seals was a profitable pursuit because of the good prices which could be obtained for their skins and oil. *It is possible that the netting method, if intensively employed, will reduce cave-frequenting species to the point of extinction in a very short time —say, in a single year.* If, therefore, rewards are to be offered for the destruction of seals in Cornwall it is, in the writer's opinion, highly desirable that a detailed survey of their ordinary haunts and breeding places be undertaken in order to assess as accurately as possible the relative abundance of the Grey and Brown species and to obtain reliable knowledge of their separate habits. If it is the Grey Seal which is abundant on the Cornish coast, the complete extermination of this attractive and interesting member of the British Marine Mammalian Fauna from a locality which, apparently, it finds congenial, seems scarcely to be desirable. Should such a survey as that suggested above be carried out, periodic return visits to the Grey Seals' ordinary haunts and breeding places (say, once a year during the breeding season) would serve to reveal the extent of the depletion which was being brought about in their numbers.

VII. SUMMARY.

1. In the course of three trips to the herring grounds in the vicinity of St. Ives five seals were sighted. Seven others were also seen at various other times and places in the course of five days spent in that locality.

2. During a single night at sea in Port Isaac Bay eight seals were sighted.

3. It was obvious from the movements of certain of the seals observed on the fishing grounds that they were attracted to the herring nets.

4. Direct evidence that the seals actually remove fish from the nets was not obtained.

5. Damage done to drift nets by seals is negligible.

6. Grey Seals (*Halichœrus grypus*) are present in considerable numbers, and are probably the commonest seals in Cornish waters.

7. Brown Seals (*Phoca vitulina*) appear to be few—they may even be rare—around Cornwall.

8. There is at least one seal colony of considerable size in certain caves near Boscastle. This appears to consist of Grey Seals. Probably other such colonies exist on the Cornish coast.

9. Clupeoid remains have been found in two out of the three Grey Seal stomachs which have been examined.

10. Further and more exact knowledge of the habits and relative abundance of Grey and Brown Seals around the Cornish coast is desirable.

VIII. APPENDIX.

DETAILED LOG OF OBSERVATIONS AND EVENTS.

Thursday, 17/11/32.

2.30 p.m. Arrived St. Ives.

3.45 p.m. Went on board M.B. *Grateful* (J. Boase, Master) which put to sea immediately for the fishing grounds.

6.05 p.m. Commenced "shooting" nets (14 in number) off Cligga Head (see Chart II). Wind NNE. Innermost (off-end) net about ½ mile from the shore.

No seals were sighted along the whole route to this fishing ground, nor did any appear within range of the lights while fishing was in progress during the night. There was thus absolutely no evidence of the presence of seals obtained during this trip.

Friday, 18/11/32. (St. Ives.)

(See Chart I.)

3.50 p.m.	Proceeded to sea in *Grateful*.
3.55 p.m.	1 seal (large brown)—sighted some distance to seaward of St. Ives Head, just outside St. Ives harbour.
4.10 p.m.	1 seal—swimming close to the rocks at Clodgy Point.
4.16 p.m.	1 seal—in small bay between Hor Point and Pen Enys Point.
4.54 p.m.	Commenced " shooting " nets off Zennor Head. Wind NNE. Innermost (near) net about ¼ mile from the shore.
5.15 p.m.	Nets all out.
	1 seal—sighted about half-way between boat and shore. (Made several appearances more or less in the same place after first seen.)
7.30 p.m.	" Looked at " nets. No herrings and " nets all on fire." Successful fishing, therefore, considered impossible. Commenced hauling.
9.15 p.m.	Boat returned to harbour.

Four seals were sighted on this trip. They are obviously fairly common around the rocks westward from St. Ives. But no seal approached the nets

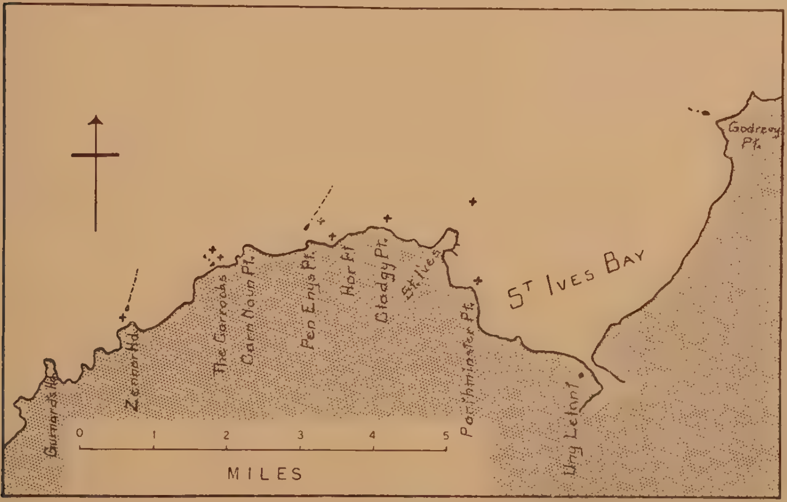
Godrevy Pt.
St Ives Bay
Gurnard's Hd.
Zennor Hd.
The Carracks
Carn Naun Pt.
Pen Enys Pt.
Hor Pt.
Clodgy Pt.
St Ives
Porthminster Pt.
Uny Lelant
0
1
2
3
4
5
MILES

Chart I.—North Cornwall Coast—Gurnard's Head to Godrevy Point.
+ = Seals seen on 18th, 19th, and 20th November.
—.—.—.—. = Position where m.b. *Grateful* shot her net on 18th (evening) and 19th (morning).

while it was still light enough to see ; and when hauled up they showed no signs of having been visited in the darkness.

Saturday, 19/11/32. (St. Ives.)

3.50 a.m. Left again for fishing ground.

4.55 a.m. Commenced " shooting " off Pen Enys Point (Chart I). Innermost (near) net about 300 yards from the shore.

5.15 a.m. Nets all out.

1 seal—appeared within circle of light cast by boat's lamps ; swimming from direction of the shore ; remained visible for short time and then disappeared in the darkness along the side of the near net.

8.35 a.m. Returned to harbour with about 700 herrings.

The single seal observed on this short trip was very definitely " making for " the nets.

2.30–6.15 p.m. Walked along the shore—eastward from St. Ives as far as Uny Lelant. Wind NNE. Heavy ground swell beginning to come in.

1 seal* (small grey)—observed at Porthminster Point, a few yards out from the rocks. No more were seen, though several reported to be in the vicinity by some boys playing on the beach.

Sunday, 20/11/32. (St. Ives.)

Walked along the cliffs—westward from St. Ives—as far as Gurnard's Head. (See Chart I.) Heavy ground swell. Wind NNE.

2 seals—seen swimming about in the sea near the Carrack Rocks.

Monday, 21/11/32. (St. Ives.)

(See Chart II.)

Hired M.B. *Grateful* for exploratory cruise along the eastern shores as far as Basset Island. The fishermen of St. Ives say that seals are usually more numerous in that locality than anywhere else in their area.† Wind N. Very heavy ground swell.

9.15 a.m. Left St. Ives harbour.

10.13 a.m. 1 seal—sighted just eastward of Navax Point.

10.35 a.m. 1 seal—playing in the surge at Hell's Mouth.

No more seals were seen on the outward journey or at Basset Island.

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* On Thursday, 17th, *a small seal*, swimming around the same rocks, was sighted from the train just before it entered St. Ives station. This may have been the same animal.

† See also p. 491 of this report.

Steered in a " wide circle " to seaward on the return journey.

11.42 a.m. 1 seal—in centre of St. Ives Bay.

12.03 p.m. 1 seal (very large grey)—playing in the breakers at Porthminster Point, just outside St. Ives harbour and to the westward of it.

Four seals (one grey) were sighted on this trip. The rough sea made it very difficult to observe dark objects amongst the waves.

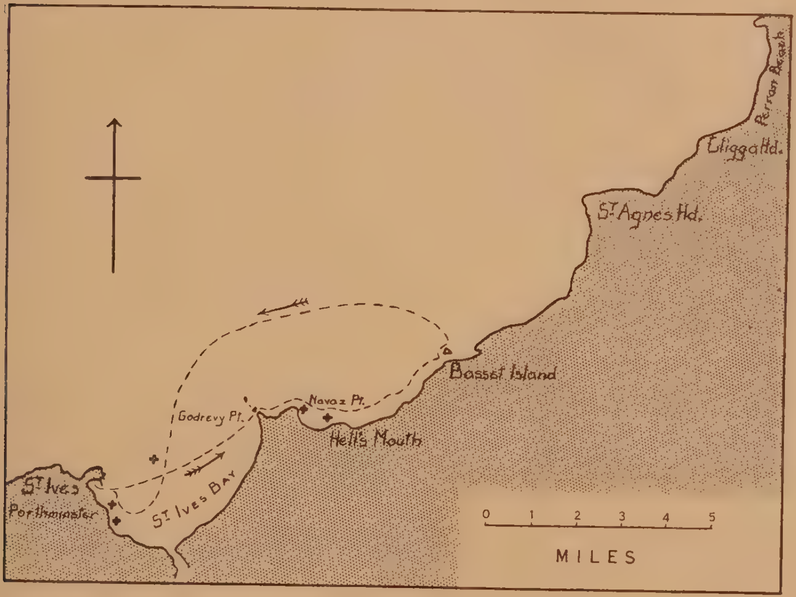
Perran Beach
Cligga Hd.
St Agnes Hd.
Bassat Island
Navaz Pt.
Godrevy Pt.
Hell's Mouth
St Ives
Porthminster
St Ives Bay
0 1 2 3 4 5
MILES

Chart II.—North Cornwall Coast—St. Ives Head to Perran Beach.
+ = Seals seen on 21st November.
— — — — = Route of exploratory voyage undertaken on that day.

3.20 p.m. Examined a large seal which had been washed up dead on Porthminster Beach. This proved to be a large female Grey Seal (*Halichœrus grypus*). The head was removed and forwarded to the British Museum where this identification was confirmed.

Stomach contents : Herring bones and some remains of herring spawn.

7.00 p.m. Left for Plymouth.

Wednesday, 23/11/32.

Proceeded to Port Isaac. Found the sea too rough there to allow the boats to go out on that evening. Remained overnight.

Thursday, 24/11/32. (Port Isaac.)

Weather still bad. Made arrangements to be recalled immediately the weather moderated sufficiently to allow fishing to be resumed, and returned to Plymouth.

Tuesday, 6/12/32.

(See Chart III.)

Returned to Port Isaac.

Went aboard M.B. *Boy Fletch* (A. Provis, Master) and put out to sea with the herring fleet which was fishing in Port Isaac Bay. (In making notes concerning the seals which were sighted on this trip it was found impossible to record their positions by reference to named points on the land. A rough sketch of the shore-line was, therefore, made, the seals numbered serially in the order in which they were sighted, and then their positions plotted as on Chart III. The additional details concerning them are given below.)

3.49 p.m. 1 seal (grey)—seaward of boat. (1)

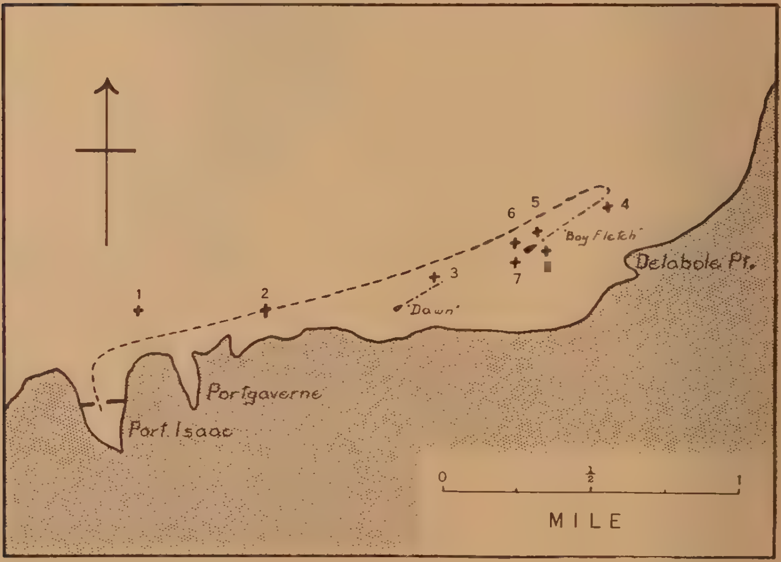

Chart III.—North Cornwall Coast—Port Isaac Harbour to Delabole Point.
+ = Seals* seen on 6th December.
—.—.—.—. = Positions of nets of *Dawn* and *Boy Fletch* on shooting.
— — — — — = Course of *Boy Fletch* to fishing ground.

* In plotting positions of the Seals the small changes in position occupied by the nets owing to drift have been ignored.

4.03 p.m. 1 seal (small grey)—rose to the surface about 20 yards ahead, right in the boat's track; dived immediately (but reappeared astern several times in the next 5 minutes). (2)

4.17 p.m. 1 seal—hard by the cork-rope of the outermost (off-end) net of another fishing boat, the *Dawn*, which was then shooting the last of her nets. (3)

4.33 p.m. Commenced shooting nets (13 in all) off Delabole Point.

4.36 p.m. 1 seal (small)—bobbed up beside the cork-rope of our first net but promptly disappeared again. (4)

4.49 p.m. 1 seal—sighted close alongside near net, about half-way along it; disappeared in the gathering dusk following the direction of the cork-rope. (5)

5.36 p.m. 1 seal (small)—close by and to seaward of boat. Possibly same as No. 4 above. (6)

7.00 p.m. Commenced hauling.

7.23 p.m. 1 seal (large)—about 6 yards behind the stern of the boat; appeared to be following her as she moved along. (7)

1 seal—also sighted at the same time by the side of the net which was then being hauled inboard, near the outermost edge of the circle of light. (Disappeared and reappeared several times.) (8)

Eight seals were sighted on this trip, six of them in the immediate vicinity of herring nets or of a fishing boat while her nets were out. There can be no doubt that seals were numerous at this time in Port Isaac Bay, and that they were attracted to the herring nets.

Wednesday, 7/12/32. (Port Isaac.)

Visited seal caves at Boscastle (see p. 492 of this report).

Friday, 9/12/32, and *Saturday*, 10/12/32.

At Sennen Cove (see p. 490 of this report).

Tunny Investigations made in the North Sea on Col. E. T. Peel's Yacht, "St. George," Summer, 1933. Part I. Biometric Data.

By

F. S. Russell,

Naturalist at the Plymouth Laboratory.

With 8 Figures in the Text.

The occurrence of the Tunny, *Thunnus thynnus* L., in the waters of the North Sea during the summer months has in recent years aroused considerable interest owing to the possibilities of sport afforded by this fish to big-game anglers. It would seem also that the majority of commercial fishermen have only recently become aware that the tunny is a regular visitor to northern waters. Our knowledge of the northern migrations of the tunny has been summarised in two publications by Le Gall (**5** and **6**), and it is evident that a careful study of the fish occurring in northern waters might do much to help in elucidating the general problem of its life-story.

In the summer of 1933, at the kind invitation of Col. E. T. Peel, D.S.O., M.C., I had the opportunity of making a preliminary survey into the occurrence of this interesting fish in the North Sea. At the same time, largely due to the reports by Mr. W. J. Clarke, F.Z.S., on the occurrence of tunny in North Sea waters, and to the successful attempts of Mr. L. Mitchell-Henry and Col. R. Stapleton-Cotton to capture them on a rod and line, there came into existence an angling club known as the "British Tunny Club." The formation of the club has attracted a number of big-game anglers to the North Sea and has given rise to further opportunities for the study of this fish, especially by the use of marked hooks.

It is a pleasure for me here to record my grateful thanks to Col. Peel for the facilities for research he afforded me and for his most generous hospitality during nearly two months' cruising on his yacht, *St. George* : I should like also to thank Col. R. Stapleton-Cotton for his great assistance in many ways and for his advice on a subject that he had already studied for several years in co-operation with well-known European biologists. To the Captain and crew of *St. George* I owe a debt of gratitude for much help willingly rendered. My thanks are also due to all members of the

British Tunny Club who have helped by marking their hooks and allowing me to have access to their fish, and especially to the Honorary Secretary, Mr. H. J. Hardy, for his help and advice. I have received also much courteous treatment from those engaged in the fishing industry and would express my feelings of gratitude to the captains and crews of the many Danish, Dutch, and British fishing vessels we boarded, and also to Mr. Bamford, Mr. Catchpole, and the Pure Ice Company at Scarborough, and Mr. Spinks and Mr. D. Buchan at Peterhead. Lastly I am deeply indebted to Mr. W. J. Clarke for much useful information he has passed on to me as a result of his many years' study of the natural history of the fishes of Scarborough. Acknowledgements are due to Mr. Victor Hey, press photographer of 1 York Place, Scarborough, for his kind permission to reproduce Figure 8.

The programme of research was divided into two main fields of enquiry :

1. A study of the fish themselves, (*a*) by marking of living fish so that if caught at a later date they might be identifiable ; and (*b*) by detailed measurements and examination of the fish caught.
2. A study of the distribution of the tunny in the North Sea in relation to hydrographical conditions.

The present report deals only with the first of these two aspects.

(*a*) *The Marking of Fish.*

It has been shown by Sella that the migrations of the tunny may be traced to some extent by a study of the occurrence of hooks in fish that have broken away from fishing-lines. On the formation of the British Tunny Club it was felt that an opportunity was afforded to help in this study by using marked hooks which could be identified again ; in this way hooks which the angler lost in fish through broken tackle might nevertheless incidentally prove of value to science if at some later date the fish in which they were fixed should be captured. Accordingly members of the club were asked to mark their hooks with three saw cuts or punch marks. This simple method was adopted as a preliminary trial to a more detailed system of marking that might be used in future years should the method prove successful.

During the fishing season of 1933 in August and September a large number of hooks have been lost in fish in the North Sea between the Dogger Bank and the Yorkshire coast. The actual number is not known but it must be at least a hundred. Many of these hooks were marked with the three saw cuts, and all are probably distinguishable by their shape and make.

I give below a list of the types of hooks that have been used and in

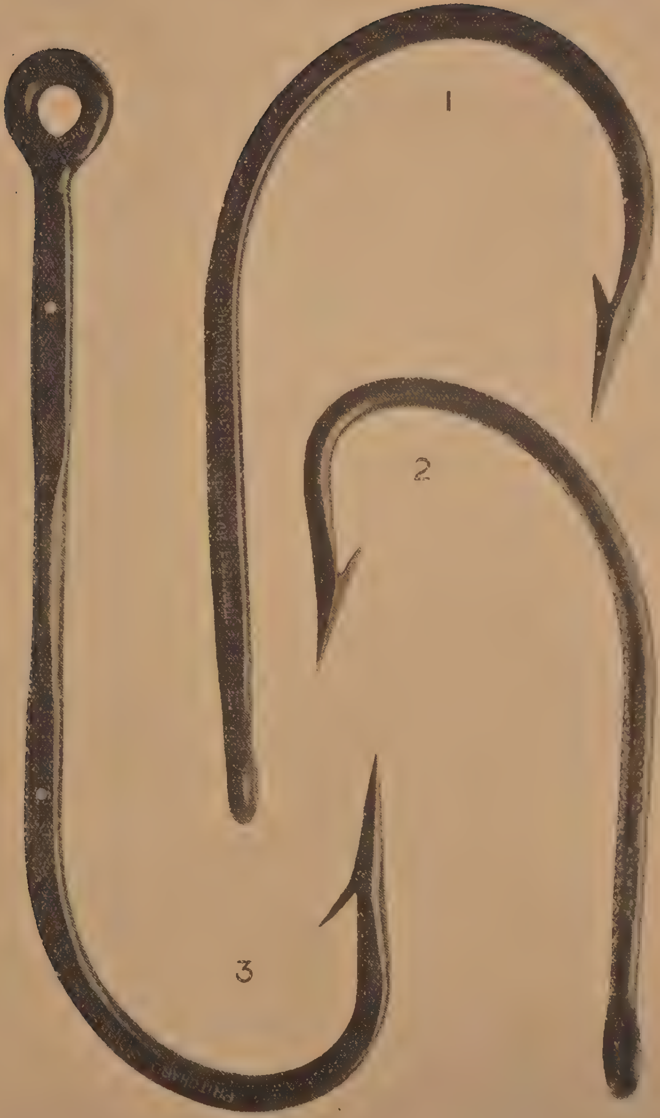

Photo. *F. S. R.*

FIG. 1.—Hooks used by anglers in the North Sea (natural size). 1. Hardy Zane-Grey; 2. Hardy Limerick; 3. Pritchard.

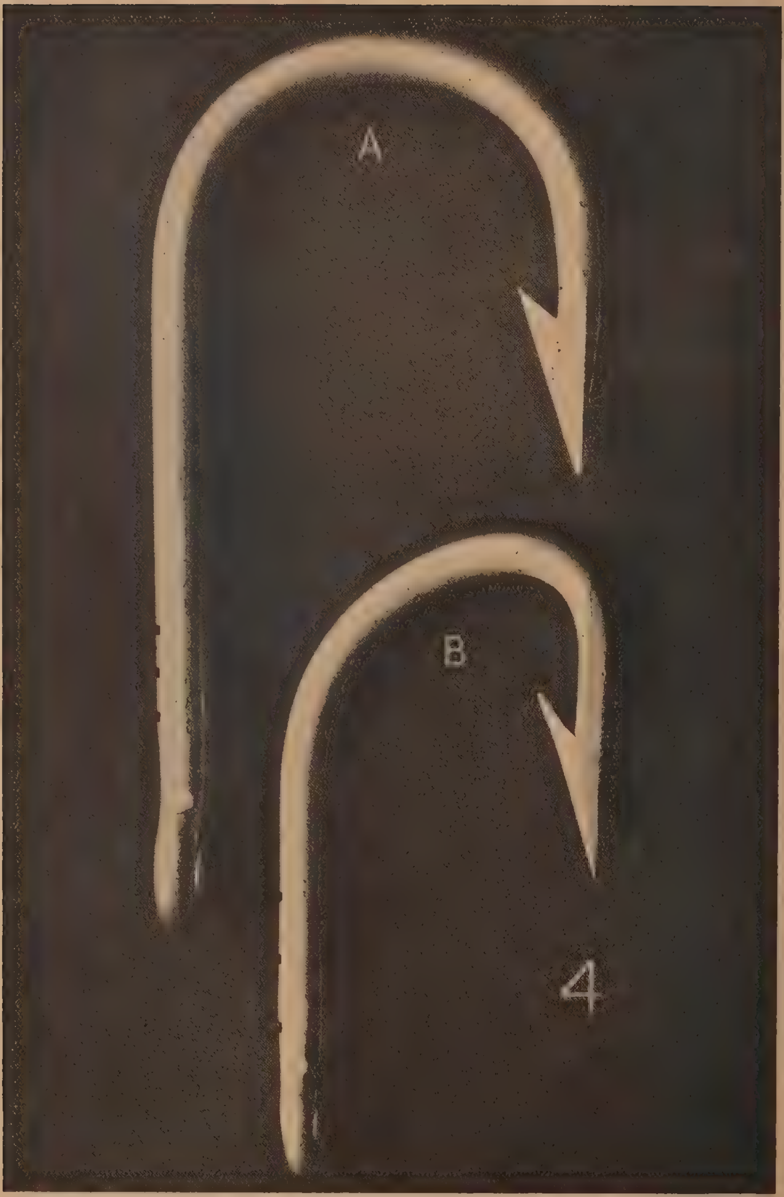

Photo. *F. S. R.*

Fig. 2.—Hooks used by anglers in the North Sea. 4. Norwegian Mustad: A, round bend; B, Limerick.

Figures 1 and 2 are given photographs of these hooks. Five kinds of hooks have been used and lost for certain.

1. Hardy Zane-Grey Hooks—Pfleuger type.
   Black hooks 4½ inches long, stamped " The Zane-Grey " on one side, and " Hardy Bros. Ltd., Alnwick, England " on the other side.
2. Hardy Limerick Hooks.
   Black hooks 4 inches long, stamped " Hardy Bros. Ltd. Alnwick " on one side, and " England " on the other side.
3. Pritchard's Hooks.
   Bronzed and steel hooks 6 inches long, with flattened sides and the name " Pritchard Scarboro " stamped on the bend on one side: there are two small holes through the shank about 1½ inches and 4¼ inches from the eye end respectively.
4. Norwegian Mustad Hooks: galvanized iron.
   A. Round Bend, 5 inches long.
   B. Limerick, 3½ inches long.

(*b*) *Measurements of the Fish.*

At a joint meeting of the International Council for the Exploration of the Sea and the International Commission for the Exploration of the Mediterranean in 1932 to discuss investigations into the biology of the tunny, a number of biometric measurements were agreed upon in the hope of obtaining information on the possibility of the occurrence of racial variations in the tunny. Some measurements of this nature had already been made by Heldt (**4**) on fish from Tunis and by Frade (**2**) on fish from Algarve on the south coast of Portugal. Frade's results showed that the fish he measured apparently differed significantly from those measured by Heldt, but the observations were insufficient to be conclusive. Both workers studied fish which were preparing to spawn.

This cruise afforded a good opportunity to make similar measurements on the migrating fish occurring in the North Sea, and great attention was paid to this side of the work to see whether either or both of the types of fish described by the above workers occurred. At the outset difficulty was experienced in deciding from the International Council Report which were the exact points of reference for some of the measurements, a matter of considerable importance in such large fish if a high degree of accuracy was to be obtained. Accordingly I give below a very detailed statement of the measurements I have made so that other workers may know to what extent their results are comparable. Measurements were made, as suggested by Frade (**2**, p. 93), with a ribbon tape that could be fixed by an awl or skewer into the centre point of the snout as a point of origin for the length measurements. The tape was graduated to half-centimetres.

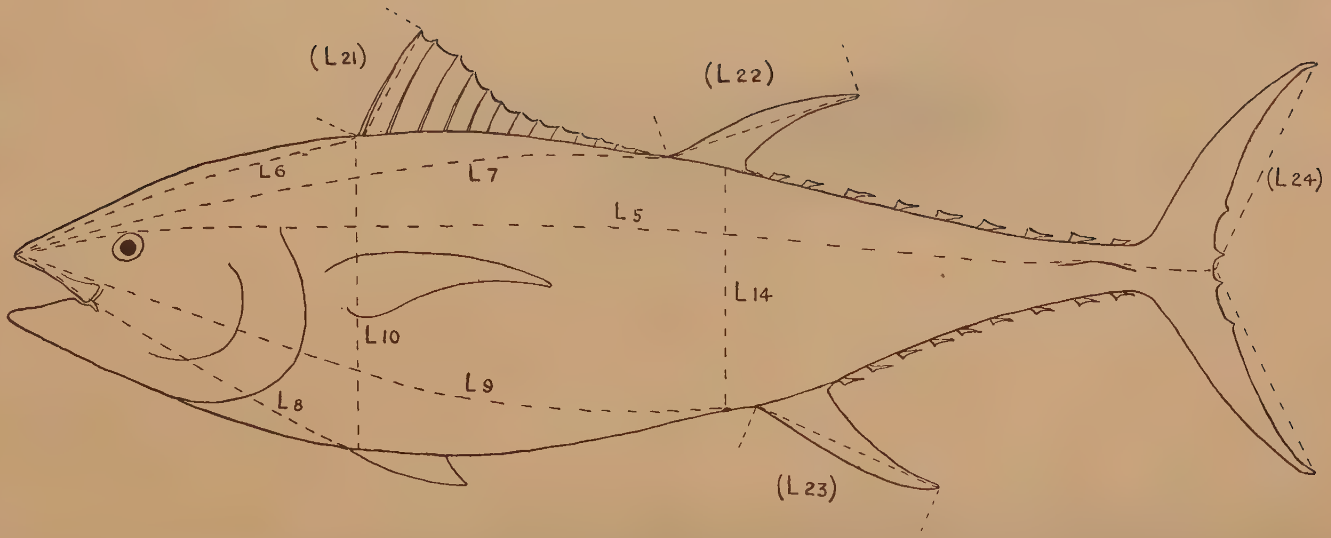
(L21)
(L22)
L6
L7
L5
L14
(L24)
L10
L9
L8
(L23)

FIG. 3.—Diagram showing body measurements made on tunny.

The notations used below for the different measurements were those given in the International Council Reports (1). See Figures 3, 4, 5, 6 and 7.

In fixing the point of origin in the centre of the snout the skewer was inserted on the most anterior point of the nose immediately above the median groove which occurs in the front end of the roof of the mouth: this ensured that it was central.

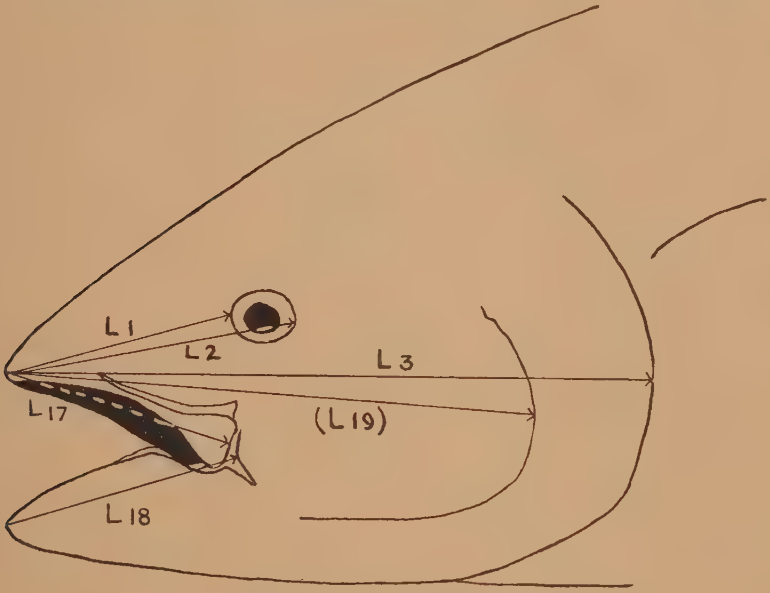

FIG. 4.—Diagram showing measurements on head.

L_1. From the origin to the anterior edge of the eye (preorbital distance).

L_2. From the origin to the posterior edge of the eye.

In the above two measurements the " eye " was taken to mean the actual eye-opening in the skin of the fish: if the eye be pushed inwards the hard edge of the skin can be clearly seen. Measurements were taken to the most anterior and most posterior points of this skin opening.

L_3. From the origin to the most distant point of the free edge of the operculum (length of the head).

In taking this measurement the soft flap of skin which extends beyond the edge of the bony operculum along its hinder margin was included; it is usually about one centimetre in width. The hindermost point of the operculum generally lay below the middle line of the body.

L_4. From the origin to the upper point of the origin of the pectoral.

Difficulty was experienced in deciding which this latter point should be. When the fin is lying flat along the side of the fish it appears to start from the point indicated A in Figure 7 ; if however the fin be fully extended at right angles to the body, the point of articulation is found to be behind A, namely, at B, Figure 7. In the measurements of the earlier fish the point B was taken as being the origin of the pectoral since A is merely the front point of a flap of skin in continuation of the flattened groove into which the fin fits. But it appeared that this point of reference might easily be confused by other workers and therefore in later fish measurements were made both to A and to B : it was found that the difference was on the average about 1·5 centimetres.

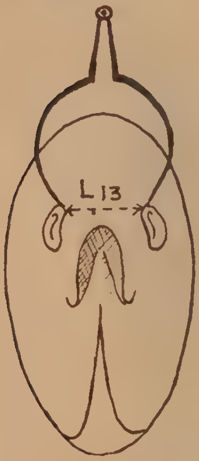

FIG. 5.—Method of measuring interorbital distance, L_{13} (after **1**).

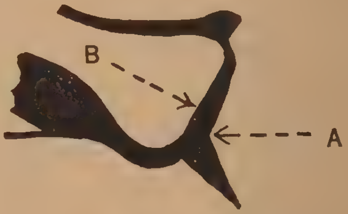

FIG. 6.—Details for jaw measurements, see Text.

L_5. From the origin to the centre of the caudal furca (length of the body).

This measurement was made by laying the tape along the body of the fish just above the eye and the pectoral fin and allowing it to lie along the body-surface and along the tail region above the lateral keel.

L_6. From the origin to the base of the first ray of the first dorsal fin.

This measurement was taken down the centre of the back to the front edge of the first spine of the first dorsal fin when fully erected, this being the shortest distance.

L_7. From the origin to the base of the first ray of the second dorsal fin.

L_8. From the origin to the base of the first ray of the ventral fin.

This measurement was made with the fin fully extended.

L_9. From the origin to the posterior edge of the anus.

L_{10}. Height of the body at the level of the first ray of the first dorsal.

Taken between upright boards.

L_{12}. Length of the pectoral fin.

This measurement presented the same difficulty as did L_4. It was decided that the fin proper started at the point B (Fig. 7); however, later a few measurements were also made from the point A with the fin pressed flat against the side of the body. The difference observed between the two measurements from A and from B was considerable, being about 5 to 5½ cm.

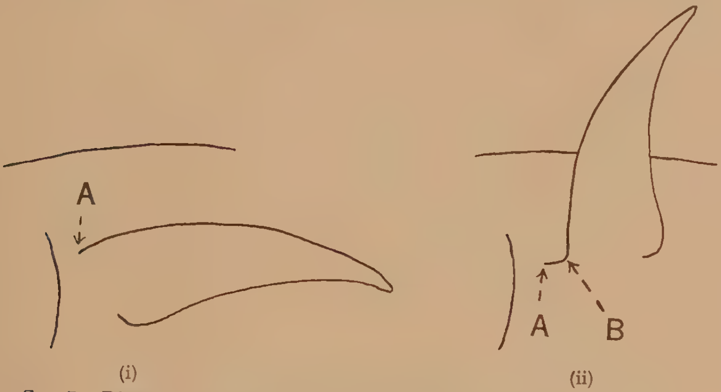

Fig. 7.—Diagram showing points of reference for pectoral fin measurements (i) with fin flat along body of fish; (ii) with fin extended.

L_{13}. Interorbital diameter (taken with calipers) (Fig. 5).

L_{14}. Height of body at level of anus (taken with calipers).

L_{15}. Interaxillary diameter.

Only a few measurements were made of this dimension owing to the difficulty of moving such heavy fish into the correct position.

L_{16}. Width of base of pectoral.

It was found that this dimension was rather unreliable as there was considerable shrinkage after a few hours due to drying.

L_{17}. Distance from the intermaxillary symphysis to the extremity of the upper jaw.

It was found that this measurement (taking the point A in Figure 6 as given in the International Commission Report Figure on p. 60) varied by as much as a centimetre between when the mouth was open and when it was shut. It seemed that the more constant point would be B, the centre point of the hind edge of the maxilla. Measurements were made in many fish both to the points A and B.

L_{18}. Distance from the mandibular symphysis to the buccal commissure.

In this measurement the point A in Figure 6 was taken as the point of reference for the buccal commissure.

(L_{19}.) From the origin to the most distant point of the edge of the preoperculum.
(L_{20}.) Length of the greatest transverse section of the lateral keels.
(L_{21}.) Height of the first dorsal fin (1st and 2nd rays).
(L_{22}.) Height of the second dorsal fin.
(L_{23}.) Height of the anal fin.
(L_{24}.) Height of each lobe of the caudal fin.

In all fish also the number of dorsal and of ventral pinnules was counted and the weights of the fish obtained.

Full details of all measurements are given in Table III, p. 521. Measurements were at first made to the nearest half-centimetre, and later, to ensure greater accuracy in the shorter dimensions, to the nearest millimetre as far as could be judged. In order to test whether a long period out of the water caused any significant shrinkage, two fish, Nos. 31 and 32, were measured immediately after capture and again several hours later. Only two measurements showed any alteration of significant magnitude, namely the length of the base of the pectoral fin which shrank by 2·5 and 1·5 cm. respectively, and the width of the lateral keels which shrank by 1·25 and 0·5 cm.: both were rather large shrinkages for such short measurements.

Biological Indices.

From the measurements obtained the following biological indices recommended in the International Reports were calculated :—

$$Oi_1=\frac{2L_3}{L_1+L_2} \qquad Oi_2=\frac{L_3}{L_2-L_1} \qquad (Oi_3)=\frac{L_3}{(L_{13})}$$

$$Ti=\frac{L_5}{L_3} \qquad (Hi)=\frac{L_5}{(L_{10})} \qquad Pi=\frac{L_5}{L_{12}}$$

$$\frac{Pi}{Ti}=\frac{L_3}{L_{12}} \qquad Di=\frac{L_5}{L_6} \qquad D^1i=\frac{L_5}{L_7}$$

$$Vi=\frac{L_5}{L_8} \qquad Ai=\frac{L_5}{L_9} \qquad H^1i=\frac{L_{10}}{L_{14}}$$

$$Ei=\frac{L_{10}}{L_{15}} \qquad P^1i=\frac{L_{12}}{L_{16}} \qquad M^1i=\frac{L_{17}}{L_{18}}$$

COMPARISON OF NORTH SEA TUNNY WITH THOSE MEASURED BY HELDT AT TUNIS AND FRADE AT ALGARVE.

In order that a strict comparison may be made between my results and those of Frade and Heldt the same statistical data have been calculated, viz.: average deviation, $\frac{\Sigma d}{n}$; probable error, $h=\pm 0{\cdot}6745\times\pm\sqrt{\frac{\Sigma d^2}{n}}$;

Probable error of the mean, $\frac{h}{\sqrt{n}}$; the practical error, $\frac{5h}{\sqrt{n}}$ and the probable and certain limits.

The full details are given in Table I, in which the data obtained by Frade and Heldt, on fish in the G_4 group (viz. 200 to 260 cm., **4**, p. 14), are also given for comparison. It will be convenient to compare each biological index in turn. All the 32 fish that I have measured were large fish between 223 and 271 cm. in length.

Oi_1: for the North Sea fish this index lies midway between those for Tunis and Algarve and the certain limits almost exactly extend over the whole range for these limits in both Tunis and Algarve fish.

Oi_2: for the North Sea fish this index is higher than in either the other two types but lies nearer that of those from Tunis and is very near that given by Heldt (**4**, p. 14) for fish 235 cm. in length.

Oi_3: North Sea fish have a lower index than the Algarve but no comparable data are available for the Tunis fish.

Ti: for the North Sea fish this index lies between that of those from Algarve and from Tunis, but is considerably nearer that for those from Algarve.

Hi: for North Sea fish lies below that for Algarve; no comparable data are available from Tunis.

Di: for the North Sea fish lies above both Algarve and Tunis fish, being nearer the Algarve type.

D^1i: lies above that for both Algarve and Tunis fish.

Vi: lies below that for both Algarve and Tunis fish, but approximates very closely to those from Algarve.

Ai: approximates very closely to that for Algarve and Tunis fish, but is very slightly lower.

The fish examined in the North Sea would thus appear to differ in body proportions both from those between 200 and 260 cm. in length measured by Frade at Algarve and by Heldt in the Mediterranean at Tunis. The first and second dorsal fins are set slightly further forward in the North Sea fish than in the Algarve and Tunis fish: the ventral fin and anus are approximately in the same position as in the Algarve fish: in the North Sea fish the head is smaller than those measured by Frade; the eye is also considerably smaller and is slightly further forward on the head resembling the Tunis fish in these respects; the interorbital width is greater.

In no respect, except in the index Oi_1, was the spread of the variations in the biological indices sufficient to cover both Algarve and Tunis fish, but it was always of the same order of those given by Frade and by Heldt.

It is useless to discuss the significance of the difference between my results and those of Frade and Heldt until far more measurements have been made of large tunny from different regions and at different times of the year. It should however be stressed that all the fish I measured lay in the upper half of Heldt's G_4 group, taken as being 200 to 260 cm.; it is possible that this may account for some of the differences observed. It is likely also that there will be slight differences in body proportions before and after spawning.

Many fish showed a tendency towards the concavity of the snout mentioned by Heldt (in **1**, p. 215): this consequent shortening of the preorbital distance is clearly shown in Figure 8 in the fish nearest the camera.

TABLE I.

COMPARISON OF BIOLOGICAL INDICES OF NORTH SEA TUNNY (223 to 271 CM. IN LENGTH) WITH THOSE OF FISH FROM ALGARVE (ATLANTIC) AND TUNIS (MEDITERRANEAN) BETWEEN 200 AND 260 CM. IN LENGTH.

		NORTH SEA.	ALGARVE. (Frade.)	TUNIS. (Heldt.)
Oi_1				
Mean (M)	=M.	2·42	2·406	2·443
Average deviation	$\left(\frac{\Sigma d}{n}\right)$=A.D.	0·044	0·053	0·049
Probable error	(h)=P.E.	±0·040	±0·049	±0·0452
Probable error of the mean	$\left(\frac{h}{\sqrt{n}}\right)$=P.E.M.	±0·007	±0·0049	±0·0045
Practical error	$\left(\frac{5h}{\sqrt{n}}\right)$=Pr.E.	±0·035	±0·024	±0·023
Probable limits	=P.L.	2·413–2·427	2·401–2·411	2·429–2·437
Certain limits	=C.L.	2·385–2·455	2·381–2·430	2·410–2·456
Oi_2	M.	11·42	9·726	10·98
	A.D.	0·470	0·623	0·73
	P.E.	±0·386	±0·553	±0·63
	P.E.M.	±0·068	—	—
	Pr.E.	±0·341	—	—
	P.L.	11·352–11·488	9·627– 9·825	10·87–11·09
	C.L.	11·079–11·762	9·231–10·221	10·42–11·54
(Oi_3)	M.	2·51	2·70	—
	A.D.	0·086	0·076	—
	P.E.	±0·073	±0·069	—
	P.E.M.	±0·013	—	—
	Pr.E.	±0·065	—	—
	P.L.	2·497–2·523	2·693–2·707	—
	C.L.	2·446–2·575	2·665–2·735	—
Ti	M.	3·74	3·713	3·87
	A.D.	0·068	0·070	0·088
	P.E.	±0·066	±0·061	±0·066
	P.E.M.	±0·012	—	—
	Pr.E.	±0·059	—	—
	P.L.	3·728–3·752	3·702–3·724	3·86–3·88
	C.L.	3·681–3·799	3·658–3·768	3·81–3·93

		North Sea.	Algarve. (Frade.)	Tunis. (Heldt.)
(Hi)	M.	4·21	4·410	—
	A.D.	0·138	0·095	—
	P.E.	±0·118	±0·086	—
	P.E.M.	±0·022	—	—
	Pr.E.	±0·120	—	—
	P.L.	4·188–4·233	4·395–4·425	—
	C.L.	4·090–4·330	4·335–4·485	—
Di	M.	3·62	3·555	3·518
	A.D.	0·085	0·063	0·077
	P.E.	±0·070	±0·048	±0·066
	P.E.M.	±0·012	—	—
	Pr.E.	±0·062	—	—
	P.L.	3·608–3·632	3·546–3·564	3·506–3·530
	C.L.	3·558–3·682	3·510–3·600	3·458–3·578
D^1i	M.	1·93	1·886	1·887
	A.D.	0·026	0·029	—
	P.E.	±0·023	±0·029	—
	P.E.M.	±0·004	—	—
	Pr.E.	±0·021	—	—
	P.L.	1·926–1·934	1·883–1·889	1·881–1·893
	C.L.	1·909–1·951	1·871–1·901	1·858–1·916
Vi	M.	3·17	3·197	3·397
	A.D.	0·098	0·081	0·087
	P.E.	±0·084	±0·072	0·074
	P.E.M.	±0·015	—	—
	Pr.E.	±0·074	—	—
	P.L.	3·155–3·185	3·185–3·209	3·383–3·411
	C.L.	3·096–3·244	3·137–3·257	3·329–3·465
Ai	M.	1·64	1·660	1·657*
	A.D.	0·022	0·027	—
	P.E.	±0·019	±0·024	—
	P.E.M.	±0·004	—	—
	Pr.E.	±0·018	—	—
	P.L.	1·646–1·654	1·658–1·662	1·652–1·662*
	C.L.	1·632–1·668	1·648–1·672	1·634–1·680*

The biological index Pi has not been considered here owing to the doubt about the correct points of reference to take in measuring the pectoral fin. It was found that when measuring from the point B in Figure 7 the mean for Pi was 6·30, and the average of the four measurements made from the point A was 5·57.

The Length of the Fins.

In Table II are given the lengths of the 2nd dorsal, 1st dorsal, and anal fins, and upper caudal lobe, expressed as percentages of the total length of the fish (L_5). In this table the lengths of the second dorsal are arranged serially in order of size and there is a very distinct tendency for the fish with short second dorsals to have short first dorsal and anal fins and to a less extent narrower tails, and for fish with long second dorsals to have the other two fins long also and the tail wider. There is considerable variation in fin-length, the range covered by the different fins being :—

---

* For (G_3+G_4) fish, i.e. 160 to 260 cm.

2nd Dorsal . . .	12·4–17·0%	of total	length,	L_5
1st Dorsal . . .	8·5–11·4%	,,	,,	,,
Anal	12·5–17·2%	,,	,,	,,
Upper Caudal Lobe . .	15·3–18·7%	,,	,,	,,

No correlation is shown between the length of the above fins and that of the pectoral fin which varies between 14·4 and 17·4% of the total length of the fish (L_5).

It is of interest also to note that the lengths of the 2nd dorsal fin show distinct bimodality, the two modes falling in the 13-cm. and the 15 to 16-cm. groups respectively. No such bimodality is however shown by other fins.

No correlation could be found between fin-length and other body proportions of the fish.

TABLE II.

Lengths of Second Dorsal, First Dorsal, Anal and Caudal Fins expressed as Percentages of Body Lengths. (Caudal Fin Based on Upper Lobe.)

Fish No.	2nd D.	1st D.	A.	C.
24	12·4	8·9	13·0	16·3
31	12·9	9·8	12·5	16·3
3	13·0	9·5	13·4	17·3
4	13·0	9·4	13·5	16·4
28	13·4	10·7	14·4	18·0
29	13·4	10·5	14·9	17·9
7	13·5	8·6	14·8	17·6
22	13·6	9·0	13·2	16·8
19	13·8	9·8	13·6	16·6
21	13·8	9·7	13·1	16·4
2	13·8	9·1	14·6	17·8
10	13·9	10·5	13·1	15·3
11	14·1	10·7	13·7	16·7
12	14·6	11·4	13·0	17·5
5	15·0	10·0	14·6	17·9
13	15·0	10·0	13·7	17·2
16	15·0	11·1	15·8	17·4
23	15·3	9·2	13·4	17·1
8	15·6	11·2	16·4	18·0
14	15·8	10·0	14·1	18·7
15	15·9	11·3	14·9	16·9
27	15·9	11·1	14·9	18·1
1	16·0	10·4	16·8	17·6
26	16·0	10·6	14·8	17·0
18	16·2	10·0	15·5	17·0
6	16·3	8·5	15·4	16·7
9	16·3	10·0	15·5	17·5
17	16·3	10·7	17·2	17·0
31	16·5	10·4	14·0	18·7
32	16·5	11·2	15·3	17·8
20	16·7	9·7	15·7	17·5
25	17·0	10·0	15·3	18·5

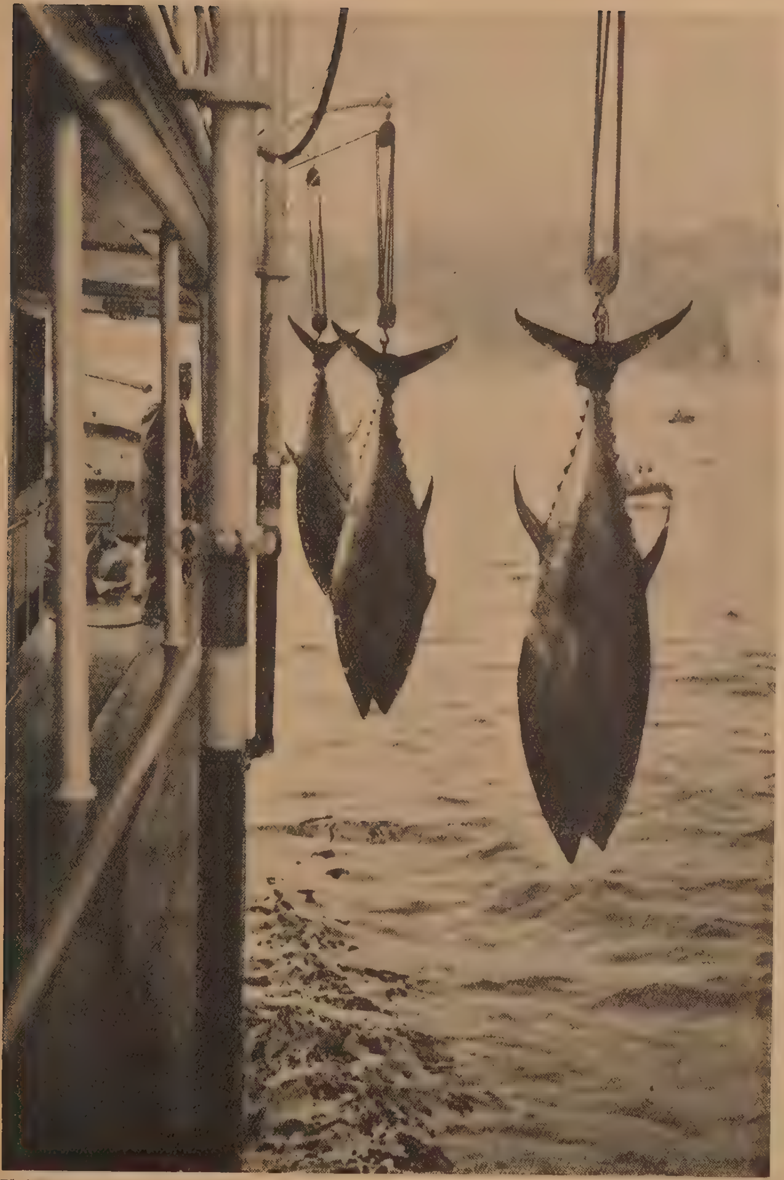

Photo *Victor Hey, Scarborough.*

FIG. 8.—Three tunny caught in North Sea, August 4th, 1933, hanging from side of M.Y. *St. George* (fishes 1, 2, and 3). Note the concavity of the snout in the fish nearest camera. (By kind permission of Mr. Victor Hey.)

DATA ON CONDITION OF FISH.

An additional series of measurements was made on the last twelve fish to give some idea of their condition. It is not easy to make an accurate measurement of the girth of such heavy fish when lying on the deck of a ship : therefore it was decided to adopt a measurement equal to half the girth taken round one side of the fish from mid-dorsal to mid-ventral lines. Owing to the obvious variation in the shape of the fish a number of these semigirth measurements were made at different points : the points of reference chosen were as follows :—

1. In the region of the front end of the first dorsal fin by slipping the tape under the pectoral fin as far forward as it would go when this fin was flat along the side of the fish : this ensured a very constant position.
2. At the anterior insertion of the second dorsal fin.
3. At the anterior insertion of the anal fin.
4. At the eighth ventral pinnule counted from the caudal end.
5. At the sixth ventral pinnule from the caudal end.
6. At the fourth ventral pinnule from the caudal end.

I am indebted to Mr. F. Hannam for suggesting the latter of these measurements. These measurements are given in Table IV, p. 522.

SUMMARY.

1. Details are given of the types of hooks lost in tunny in the North Sea in the summer of 1933.

2. Data are given on the measurements made on thirty-two large migrating fish caught in the North Sea in August and September, 1933.

3. In certain body proportions the tunny measured differ from those in the G_4 Group (200 to 260 cm. in length) given by Heldt for fish from Tunis and by Frade for fish from Algarve on the south coast of Portugal, while in some characters they resemble the Tunis fish and in others the Algarve fish, but all the North Sea fish were between 232 and 271 cm. in length.

4. It was found that there was a tendency for fish with short second dorsal fins to have short first dorsal, anal, and caudal fins, and for those with long second dorsals to have these other three fins long.

5. Measurements were made to supply data on the condition of the fish.

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DATE AND PLACE OF CAPTURE, ETC., OF THE THIRTY-TWO TUNNY FROM THE NORTH SEA MEASURED SUMMER, 1933.

All fish were caught on a rod and line except when otherwise stated.

FISH NO.	CAUGHT BY.	DATE OF CAPTURE.	POSITION.		DATE AND PLACE OF MEASURING.	
1	Col. Cotton	4.viii.33	55°34′N.	3°26′E.	5.viii.33	on board.
2	On pellet (*St. George*)	,,	,,	,,	,,	,,
3	Col. Peel	,,	,,	,,	,,	,,
4	On pellet (*St. George*)	7.viii.33	55°18′N.	2°49′E.	8.viii.33	,,
5	Col. Cotton	,,	,,	,,		
6	Lady Broughton Lord Moyne	4.viii.33	55°19′N.	2°28′E.	9.viii.33	in Pure Ice Co. Factory.
7	F. Hannam, Esq.	26.viii.33	54°51′N.	0°19′E.	26.viii.33	on board.
8	L. Mitchell Henry, Esq.	,,	,,	,,	,,	,,
9	,, ,, ,,	,,	,,	,,	,,	,,
10	Col. Cotton	,,	,,	,,	,,	,,
11	Col. Peel	,,	,,	,,	,,	,,
12	On pellet (*St. George*)	,,	,,	,,	,,	,,
13	Col. Cotton	,,	,,	,,	,,	,,
14	Mrs. T. O. M. Sopwith	,,	55°05′N.	1°30′E.	28.viii.33	in fish market.
15	T. O. M. Sopwith, Esq.	,,	55°10′N.	1°00′E.	,,	,,
16	Miss G. Yule	,,		—	,,	in Pure Ice Co. Factory.
17	S. V. Hine, Esq.	,,	54°51′N.	0°19′E.	,,	in Mr. Bamford's cellar.
18	David Leigh, Esq.	,,	,,	,,	,,	in exhibition room.
19	E. Leigh, Esq.	,,	,,	,,	,,	,, ,,
20	Col. Cotton	29.viii.33	54°57′N.	0°50′E.	29.viii.33	on board.
21	,, ,,	,,	,,	,,	,,	,,
22	,, ,,	,,	,,	,,	,,	,,
23	On pellet (*St. George*)	,,	,,	,,	,,	,,
24	Col. Cotton	,,	,,	,,	,,	,,
25	,, ,,	30.viii.33	54°55′N.	0°25′E.	30.viii.33	,,
26	Col. Peel	,,	54°55′N.	,,	,,	,,
27	,, ,,	,,	,,	,,	,,	,,
28	On pellet (Col. Peel)	,,	,,	,,	,,	,,
29	Col. Peel	2.ix.33	54°48′N.	0°28′E.	2.ix.33	,,
30	,, ,,	,,	,,	,,	,,	,,
31	,, ,,	,,	,,	,,	,,	,,
32	Col. Cotton	,,	,,	,,	,,	,,

TABLE III.

MEASUREMENTS OF TUNNY FROM THE NORTH SEA: ALL MEASUREMENTS ARE IN CENTIMETRES.

NO. OF FISH.	1	2	3		5	6	7	8	9	10	11	12	13	14	15	16
L_1	25	27	22	21½	23½	25	27	24	24	22½	23	25	24	25	25	25
L_2	31	33	28	27	29	31	33	29½	29½	28	28½	31	30	31	30½	31
L_3	68	71	62·5	60	65	62	70½	66	65	62	63	67	68	69	67	68
L_4	69	73	64	62	66	70	75	67½	66½	65	65½	69	69	69½	69	71
L_5	250	253	231	223	240	246	266½	250	245	248	233½	246	256	241	252	253
L_6	67	73	65	61½	63½	71	72	66½	66½	63½	62	69	70	69	70	73
L_7	129	133	121	117	121	131	136	128	126	121	120	130	137	126	130	131½
L_8	82	81	73	69	79	81	90½	79	76	73½	76½	75½	76	81	79	81
L_9	154	151	139	135	144	152	166	154	147	143½	143	151	156	147	149½	154
L_{10}	59	64	56	48	56	62	68	63	58	57	56	54	60	60	61	60
L_{12}	40	42	38	36½	41	40	42	39	38½	40	34	41	40	40	38½	44
L_{13}	27	29	23	23½	25½	27	30	26	26½	24	24	26	26	25	25	28
L_{14}	45	46	45	41	45½	47	50½	50	45½	46	45½	43	50½	46½	51½	46½
L_{15}	40	42	39	40	40	41	–	43½	–	–	–	–	–	–	–	–
L_{16}	14	16	15	12½	13	13	15	14	14	13	12	14	13½	14	13½	13
L_{17}	26	27·5	23	23	26	27	27	25	24½	24	25	26	27	27	26	25
L_{18}	26	27	23	22	26	25	29	26	24½	23	24½	25	26	26	25	24½
(L_{19})	54·5	57	50	48	52½	55	58	54	51½	50	50	53½	56	54½	54½	55
(L_{20})	18	18	17	17½	18	17	20	**	17½	19	19	20	19	17½†	18½	18½
(L_{21})	26	23	22	21	24	21	23	28	24½	26	25	28	25½	24	28½	28
(L_{22})	40	35	30	29	36	40	36	39	40	34½	33	36	38½	38	40	38
(L_{23})	42	37	31	30	35	38	39½	41	38	32½	32	32	35	34	37½	40
(L_{24}) Upper	44	45	40	36½	43	41	47	45	43	38	39	43	44	45	42½	44
(L_{24}) Lower	44	45	40	36½	43	41	46	45	43½	38	39	43	42	45	42½	44
Fin formula																
Pinnules D.	10	10	10	10	10	10	10	–	–	10	11	5+3	10	10	10	10
Pinnules V.	9	9	9	9	9	9	9			10	10	9	9	9	9	9
Weight (lbs.)	524	542	459	–	461	532	705	532	514	511	476	434	616	505	575	561

NO. OF FISH.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
L_1	22	27½	23	26·4	26·9	24·3	26	24	27·5	24·5	24·75	25	26·5	25·2	26	24·8
L_2	28	33½	29	32·2	32·8	30·2	32·4	30	33·7	30·2	30·25	31	32·8	31	32	30·2
L_3	62	73½	63	71·7	71	66	69	64·7	73·2	67·5	66	68·8	71·5	69·5	68·5	64
L_4	63½	76	65	71·9* 73	72* 73	68* 69·5	70* 71·5	– 67	73·4* 75	68·5* 70	66* 67·5	69* 70·5	71·5* 73·2	69·5* 71	68·7* 70	64·5* 66
L_5	233	271	235	260·5	268	250·5	251	242	270·5	264	248	261	268	264*p*	257	236
L_6	66	73½	66½	74	73·25	71·5	70	68	75	72·3	70·25	72·5	75	71	71	66
L_7	123	140	123	134·5	139·5	128	132·5	125·5	141	135	129	137·5	139	134	133	124
L_8	71½	96	74	81·5	81	81	78	76·5	85·5	79	76·5	79	83·5	80	78·5	76
L_9	140	170	142	157	163	150	151	145	164	157·5	151	159	163	155	155	148
L_{10}	55	–	–	63	65	59	57	55	68	65			62	62	60	55
L_{12}	39	40	39	41·5	41·5	36	38·5	37·5	42·5	40·5	40	40	45·5* 40	46·5* 41	47* 41·5	45* 40
L_{13}	24½	29	25	29	29·5	26	28	27	31·2	26	26	28	27	27·5	28	27
L_{14}	44½	53	44½	48·5	49	45	41·5	46	54	52	47	52	51·5	51·5	51·5	49
L_{15}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
L_{16}	12	15	13	14·75	14	14	12·5	13	15·3	14·5	14	15	16	15	15·5	13
L_{17}	24½	30½	25	27*o* 26*s*	28*o* 27*s*	27*o* 26*n*	26·5*s*	25·5*o* 25*n*	28*o* 27·5*n*	26*o* 25·5*n*	25·5*o* 25*n*	25*s* 25*n*	27·5*o* 27*n*	26·5*o* 26*n*	26·5*o* 26*n*	25·5*o* 24·5*n*
L_{18}	23½	29	24	26*o* 25·5*s*	26	26*o*	25	24	26·5	25	24·5	25	26	25·5	25	24
(L_{19})	49½	60½	52½	58	58	52·75	56	52·3	60	54·5	53	56	57	56	55·5	53
(L_{20})	17	½ missing	16	19	20	18	20·5	17·5	21·8	20·2	20	20	21·75	21·5	20	17
(L_{21})	25	27	23	25	26	22·5	23	21·5	27	28	27·5	28	28	26	26·75	26·5
(L_{22})	38	44	32½	43·5	37	34	38·5	30	46	42·3	39·4	35	36	34	42·5	39
(L_{23})	40	42	32	41	35	33	33·5	31·5	42	39	37	37·5	40	33	36	36
(L_{24}) Upper	39½	46	39	45·5	44	42	43	39·5	50	45	45	47	48	43	48	42
(L_{24}) Lower	40	46	39	45	44	42	44	39·5	50·5	45	45	47·5	48	43	48	42
Fin formula																
Pinnules D.	10	10	11	10	10	11	10	10	4+5	10	10	11	10	11?	10	10
Pinnules V.	9	9	9	9	9	9	9	9	9	9	9	10	9	9?	9	9
Weight (lbs.)	428	763	456	643	735	492	546	469	714	664	549	695	709	659	687	554

** One side missing. † damaged.

* With pectoral fin flat by side (to point A, Fig. 7); other measurements to point B (Fig. 7).

L_{17}, L_{18}: *o* : mouth open, *s* : mouth shut } to point A, Fig. 6.
n : to point B, Fig. 6.

TABLE IV.

BODY MEASUREMENTS TO STUDY CONDITION OF FISH.

FISH NO.	7	8	9	10	11	12	13	14	15	16	17	18	19
6th Pinnule	40	34½	38	35	36	32½	39	34	38	37	36	41	32½
4th Pinnule	27½	24	26	25	25½	25	27½	24	26	26	27	29	22½

FISH NO.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1st Dorsal	–	–	–	91	95	83	87	84	90	89	87	90·5	91·5	90·5	91	86
2nd ,,	–	–	–	77	87	69	73	70	80	79	72	79	80	78	83	75
Anal	–	–	–	67	72	59	62	62	69	71	62	69	70	70	72	64
8th Pinnule	–	–	–	55	62	44	50	50	51	52	48	56	58	54·5	55	50
6th ,,	36	41	32½	40	45	36	39	34	39·5	39	35	44	43½	40	41	39
4th ,,	27	29	22½	28	29	26	29	24	29	28	26	29	30	28·5	29·5	28

Rissoid Larvæ as Food of the Young Herring. The Eggs and Larvæ of the Plymouth Rissoidæ.

By

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Naturalist at the Plymouth Laboratory.

With Plates I–IV.

The free-swimming young of the Rissoidæ are particularly important in the plankton for there is always one or more species present in any month and they usually occur in great abundance. The various species live between tide-marks, in the laminarian and coralline zones and in deeper water in several fathoms depth ; wherever tow-nettings are taken they usually contain some species of this family. The inshore waters, however, are the richest in rissoids. Even in winter certain species are common round the Plymouth coasts. Some years ago it was found that very young herring just before losing the yolk-sac and about a fortnight old had been eating small rissoids, evidently almost newly hatched (Plate I, Fig. 1). The herring up to a length of about 12 mm. and just after the yolk-sac had disappeared altogether continued to eat them but usually after this size they ate only small crustacea. From 1917 to 1921 it was found that out of 140 young herring examined, 91 had fed on these small gastropods. In later years they were also found feeding on them (Lebour, 1921, 1924). Other minute planktonic organisms were eaten, including algæ, tintinnids, copepod and cirripede nauplii and very small adult copepods ; also a minute bivalve larva but no other gastropod, although other veligers were present in the plankton, *Patella* being specially common. The young herrings hatch out from December to February, therefore these little gastropods must also hatch at this time and this proves to be the case for in the plankton there are large numbers of these very young veligers (Plate I, Figs. 7–8). Later on, in spring, older stages of the same mollusc abound and are quite the commonest veligers in the plankton near the coast (Plate I, Figs. 17–19). In the summer they have almost entirely disappeared.

In order to find out the species it was necessary to make a research on the eggs and larvæ of all the Rissoidæ available. It is now proved that the larva which the herrings eat is *Rissoa sarsii* Lovén. I have to thank

Mr. R. Winckworth for confirming this identification. *Rissoa sarsii* is not known from Plymouth in the adult state, although repeatedly sought, but later larvæ in plunger-jars grew up into this species. Its habitat should be just below low-water mark (Forbes and Hanley, 1853, Vol. III; Jeffreys, 1867, Vol. IV) and it is probably in a region difficult of access, being just too far out for hand collecting and too far in for dredging. The species, it is now discovered from the Plymouth larvæ, has a characteristic sculpture on the embryonic whorls and it is easy to differentiate it from other near relatives. It is also found, however, that *Alvania punctura*, living further out, has similar sculpture on the extreme apex although it is easily separated from *R. sarsii* by its other embryonic whorls and it breeds in quite a different season (Plate IV, Figs. 1–7). The sculpture on the apex, not noted by previous workers, points to a very close relationship.

The following is a list of the known Plymouth Rissoidæ, new records being marked with a cross. Some early records are of dead shells only which have not been recorded again. The names are according to Winckworth's recent list of British Marine Mollusca (1932); when these differ from those in the Plymouth Fauna List (Mar. Biol. Assoc., 1931) the latter are added in brackets.

Rissoidæ. Genus **Cingula.** Sub-genus Parvisetia, *Cingula fulgida* (J. Adams); × *C. alderi* (Jeffreys). Sub-genus Hyala, *Cingula vitrea* (Montagu) (=*Onoba vitrea*), dead shells only; *C. proxima* (Forbes and Hanley) (=*Onoba proxima*), dead shells only. Sub-genus Onoba, *Cingula semicostata* (Montagu) (=*Onoba candida*). Sub-genus Cingula, *Cingula semistriata* (Montagu); *C. cingillus* (Montagu).

Genus **Alvania.** Sub-genus Manzonia, *Alvania crassa* (Kanmacher). Sub-genus Alvania, *Alvania cimicoides* (Forbes), dead shells only; *A. cancellata* da Costa, dead shells only; *A. zetlandica* (Montagu), dead shells only (=*Manzonia zetlandica*). Sub-genus Galeodina. *Alvania carinata* (da Costa), dead shells only. Sub-genus Actonia. *Alvania punctura* (Montagu) (=*Arsenia punctura*).

Genus **Rissoa.** Sub-genus Turboella. × *Rissoa sarsii* Lovén; × R. *inconspicua* Alder; *R. parva* (da Costa); *R. guerini* Récluz. Sub-genus Rissoa, *Rissoa membranacea* (J. Adams).

Genus **Barleeia.** *Barleeia unifasciata* (Montagu) (=*Barleeia rubra*).

Of these the eggs have been obtained from *Cingula semicostata*, *C. semistriata*, *Alvania punctura*, *Rissoa inconspicua*, *R. parva*, *R. guerini*, *R. membranacea* and *Barleeia unifasciata* and the planktonic egg-capsules of *Rissoa sarsii* have been identified. The larvæ of all these have been distinguished. The veliger stage of *Cingula semicostata* and *Barleeia unifasciata* is passed within the egg and the young emerges crawling. *Rissoa sarsii* is the only species so far known with planktonic egg-capsules.

The remainder all lay lens-shaped egg-capsules deposited on some substratum which may be regarded as typical of the family.

Jeffreys (1867) states that in Rissoa " the spawn cases are solitary and hemispherical," including in the genus all those now placed in the family Rissoidæ by Winckworth. Jeffreys describes the egg-capsules of *Rissoa albella* thus : " the spawn cases are generally solitary, semiglobular and light yellowish brown ; the fry emerge from a large round hole at the top which appears when they are developed." In his account of the spawn of prosobranchs Lamy (1928) only mentions that of *Rissoa membranacea* described by Fischer (1892) and of *Rissoa parva* described by Jeffreys (1867), Caullery and Pelseneer (1910) and Pelseneer (1911). This appears to be all that is known of the spawn of any of the Rissoidæ and these three species *R. membranacea*, *R. parva* and *R. albella* have the typical capsules. The larvæ on hatching have a simple shell consisting of rather more than one whorl, and a well-developed bilobed velum. Until now few observations have been made on the older larvæ.

In the Laboratory *Rissoa membranacea* laid eggs on *Zostera*, so also did *R. parva*, *R. guerini* and *Cingula semistriata* as well as on other weeds and on the sides of a glass bowl, *R. inconspicua* on weeds and on one another, *Alvania punctura* on one another. *Cingula semicostata* laid them singly attached to bits of sand or debris in a glass jar and *Barleeia rubra* laid single eggs in tough capsules on weed in a bowl. If we examine the mode of life of these species we find that the six species with typical egg-capsules all live on weed with the possible exception of *Alvania punctura.* It is difficult to be certain of the true habitat of the last species as it is usually found in dredgings where it falls into the fine mud or sand at the bottom. *Rissoa membranacea* appears always to live on Zostera and since the disease of this plant during the last few years it has disappeared from the Plymouth coast. *R. parva* lives on many weeds, especially the large fronds of Laminaria, *R. guerini* also lives on various weeds, especially *Rhodomela subfusca** and Codium, *Cingula semistriata* on various weeds and stones below low-water mark. *R. inconspicua* is usually to be found among weeds and on shell gravel below low-water mark, *Cingula semicostata* on muddy sand and under stones between tide-marks and below low-water mark, *Barleeia unifasciata* at extreme low tide, especially on Fucus and *Calliblepharis jubata*, often with *Rissoa parva.*

The existing classification of the Rissoidæ is very unsatisfactory. Even Thiele (1929) does not notice the embryonic sculpture of our British forms (except *Alvania cimicoides* which he places in the section *Alcinulus* in the sub-genus *Alvania*), although there are certain rissoids described from Australia which have spirally ribbed apices (Thiele, Powell (1930) and

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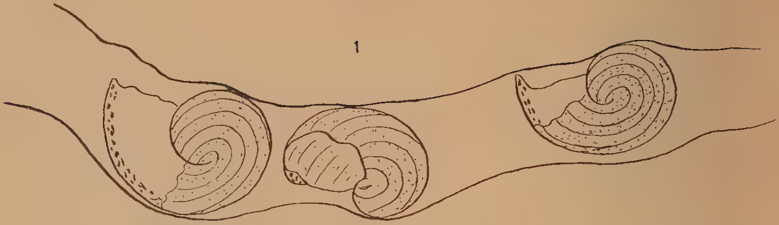
* I am indebted to Mrs. D. P. Wilson for the names of the seaweeds.

PLATE I.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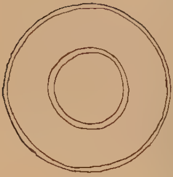
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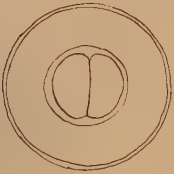
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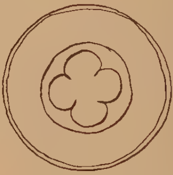
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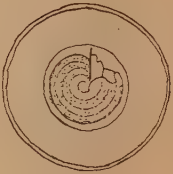
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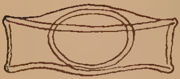
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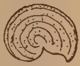
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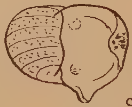
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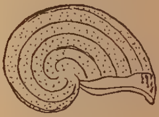
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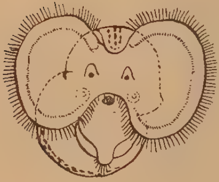
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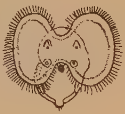
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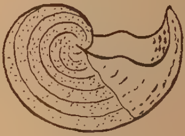
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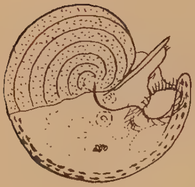
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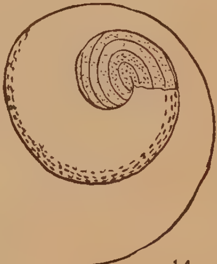
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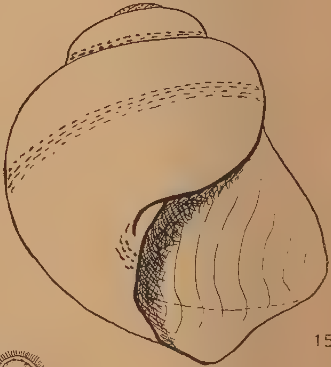
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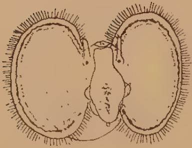
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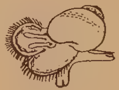
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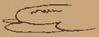
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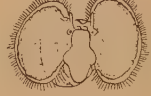
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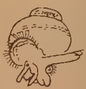
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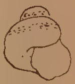
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others). A smooth apex is the commonest, such as *Rissoa membranacea*, *R. parva*, *R. guerini*, *R. inconspicua*, *Cingula semistriata* and *Barleeia unifasciata*. *Cingula semicostata* has a finely spirally sculptured apex, whilst *Rissoa sarsii* and *Alvania punctura* have spirally sculptured apices with dots in between which are so alike that except for size one could scarcely tell the newly hatched veligers apart should they occur together, which they do not. Surely this must mean a closer relationship than is generally supposed. It would be consistent to place *Rissoa sarsii* and *Alvania punctura* at least in the same genus and to remove *Cingula semicostata* from the genus *Cingula* for not only is *Cingula semistriata* very different in the apex, it also, as is well known, possesses three posterior tentacles instead of one. A detailed revision of the genus, both anatomical and conchological, is evidently highly desirable, and one which is helped enormously by the study of the larval stages. Jeffreys (1867) remarks that the embryonic whorls are important and frequently describes them. His only references to sculptured apices in the Rissoidæ are, however, in *R. Jeffreysii*, " the top whorls may be seen to have a few spiral rows of salient and re-entering angles, which last prefigure the cancellated structure of the adult shell," and further on, " the apex is marked with a Vandyke pattern instead of having rows of punctures " (as in *Rissoa punctura*), and in *Rissoa punctura* " the uppermost whorls exhibit under the microscope a few rows of punctures." *Rissoa cimicoides*, *R. Jeffreysia* and *R. punctura* are all now placed in the genus *Alvania*.

The form of the larval shell of the Rissoidæ is very like that of Lacuna, but the later stages can be distinguished by the shape of the end of the foot, in rissoids pointed, in Lacuna with two lobes. The rissoids have

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EXPLANATION OF PLATES.

(The figures are drawn to three scales, B six times A, C twice A)

PLATE I.

Rissoa sarsii.

(Figs. 1–15 scale B, 17 scale C, 16, 18–20 scale A.)

FIG. 1.—Very young larvæ in the intestine of a young herring before completely losing the yolk sac.

FIGS. 2–6.—Pelagic egg-capsules, 0·18 mm. across, (2, 6) newly laid; (3,4) dividing; (5) with larva ready to hatch. Larval shell 0·08 mm. across.

FIGS. 7–8.—Newly hatched larva, shell 0·08 mm. across.

FIG. 9.—Shell of slightly older larva, 0·15 mm. across.

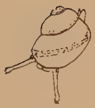
FIGS. 10–13.—Older larvæ.

FIGS. 14–15.—Shells of older larvæ.

FIGS. 16–20.—Late veligers, shell 0·48 mm. high.

FIG. 21.—Foot showing posterior process.

PLATE II.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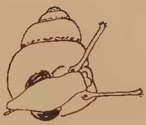
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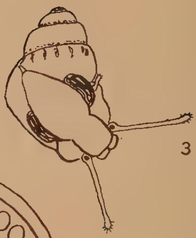
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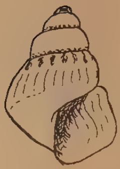
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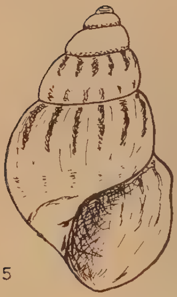
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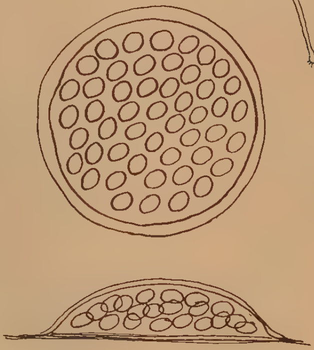
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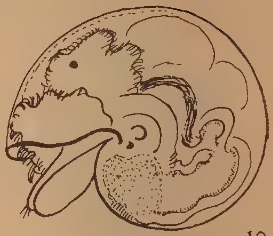
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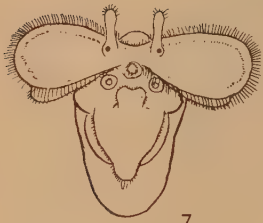
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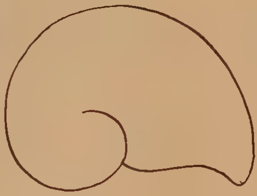
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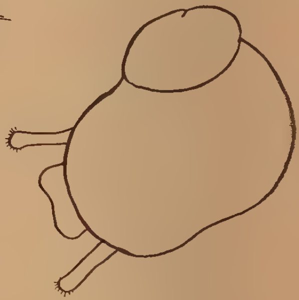
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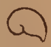
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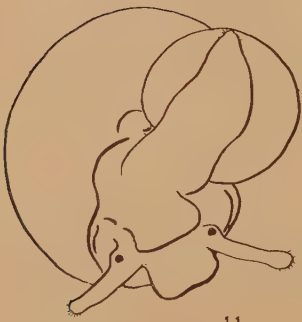
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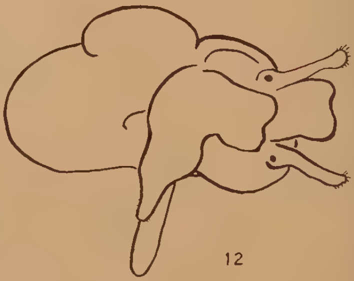
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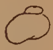
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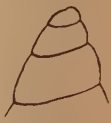
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a posterior tentacle, sometimes three, behind the operculum and above the foot, and a pendent tentacle at the upper junction of the inner and outer lip. This last is rarely absent, and in these cases probably has either escaped notice or the species should be placed elsewhere. The various larvæ can be distinguished by the size, absence or presence of sculpture on the embryonic whorls, absence or presence of colour on the velum, length of life in the plankton and general appearanc. Those which remain for some time in the plankton usually have 3 to 3½ whorls before losing the velum, the posterior and mantle tentacles then being formed and the foot assuming the adult shape.

The following shows the seasonal breeding actually observed at Plymouth :—

January : *Rissoa membranacea*, *R. parva*, *R. sarsii*, *Cingula semicostata.* February : *Rissoa membranacea*, *R. parva*, *R. guerini*, *R. sarsii*, *Cingula semicostata.* March : *Rissoa membranacea*, *R. parva*, *R. guerini*, *R. sarsii*, *Cingula semicostata.* April : *Rissoa parva*, *R. guerini*, *R. sarsii*, *Cingula semicostata*, *C. semistriata*, *Barleeia unifasciata.* May : *Rissoa parva*, *R. guerini*, *R. sarsii*, *Cingula semistriata*, *Barleeia unifasciata.* June : *Rissoa parva*, *Cingula semistriata*, *C. semicostata.* July : *Rissoa guerini*, *Cingula semistriata.* August : *Rissoa guerini*, *Alvania punctura*, unknown rissoid. September : *Rissoa parva*, *R. guerini*, *Alvania punctura*, unknown rissoid. October : *Rissoa parva*, *R. guerini*, *R. inconspicua*, *Alvania punctura.* November : *Rissoa parva*, *R. guerini*, *R. inconspicua*, *Alvania punctura*, unknown rissoid. December : *Rissoa parva*, *R. guerini*, *R. sarsii*, *R. membranacea*, *Cingula semicostata.*

RISSOA MEMBRANACEA (J ADAMS).

(Plate II, Figs. 6–15).

The largest of the Plymouth rissoids, usually occurring abundantly on *Zostera marina* on the Zostera beds. Egg-capsules of typical lens-like form, flat on the attached surface, rounded above. Actually seen from

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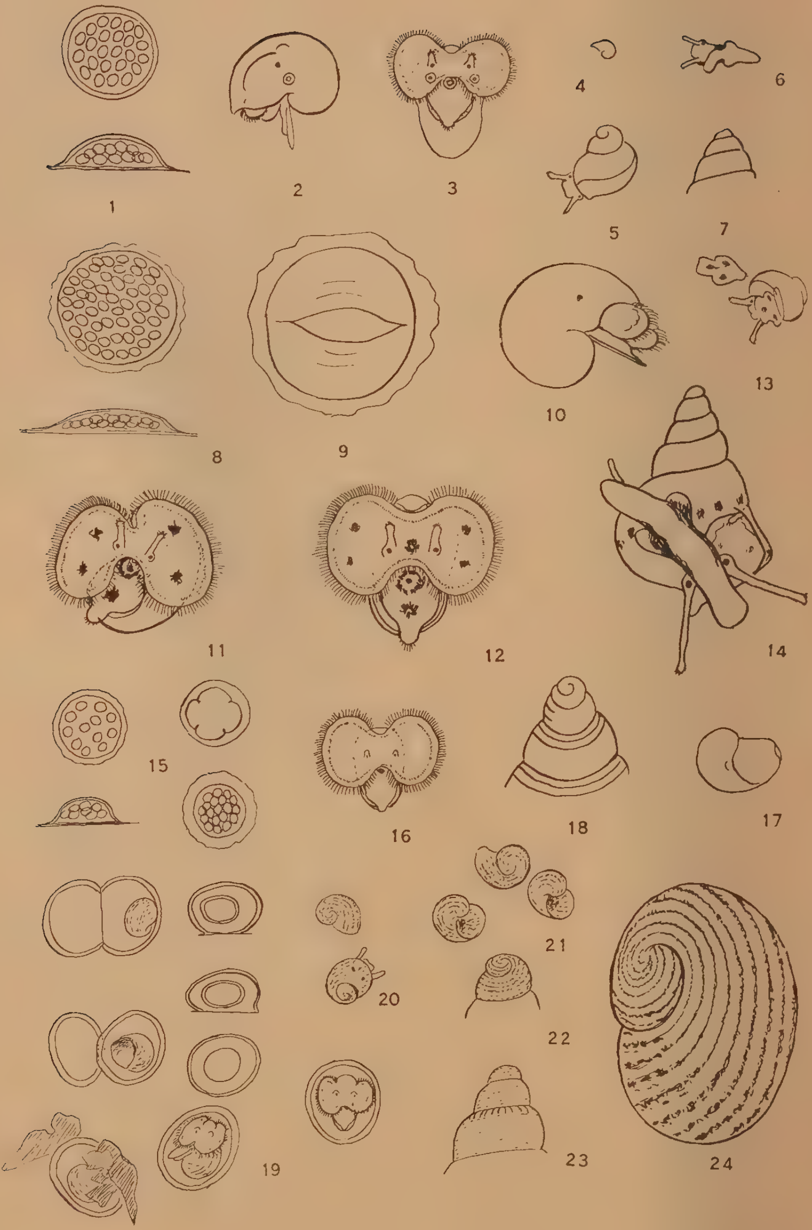
PLATE II.

Rissoa sarsii, *Rissoa membranacea.*

(Figs. 1–6, 8–15 scale A ; 7–13 scale B.)

FIGS. 1–5.—*Rissoa sarsii* reared from planktonic larvæ, shell 0·48 mm. to 2 mm. high.
FIGS. 6–15.—*Rissoa membranacea.*
FIG. 6.—Egg capsule, 1·5 mm. across.
FIGS. 7–8.—Newly hatched larva, shell 0·32 mm. across, from egg.
FIGS. 9–10.—Larvæ a few days old, reared in bowl.
FIGS. 11–14.—Young crawling, reared in bowl, shell 0·37 mm. across.
FIG. 15.—Apex of adult shell.

PLATE III.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December to March but breeding probably goes on through spring and summer as it does on the French coast. Some eggs were laid on Zostera in bowls during December and January. Fischer (1892) figures the spawn from Arcachon and describes it as watch-glass shaped, about 1·5 mm. across, with about 100 eggs, which, when ready to hatch, escape from a hole at the top formed when the larvæ are developed sufficiently to swim away. The Plymouth specimens agree in size, capsules 1·4 to 1·6 mm. across, 0·32 mm. high (Plate II, Fig. 6), but do not contain so many eggs. From 40 to 60, about 0·13 mm. across, is the usual number, and these did not all develop, several being apparently devoured by their neighbours. This may or may not be a case of true " nurse " eggs, for possibly the eggs in captivity were abnormal. In about 10 to 12 days the eggs hatched as free-swimming veligers, 0·32 mm. across the round, transparent and colourless shell of about 1½ whorls without sculpture (Plate II, Fig. 7). Animal, including velum, colourless, velum 0·32 mm. across, foot short, not reaching behind to end of shell, front part with process but not reaching mouth. Tentacles, eyes, otocysts and mouth well developed. The larvæ in a bowl with Nitzschia grew very quickly, front of foot soon covering mouth and in about 3 weeks or less were crawling, having lost velum. Larvæ hatched December 12th were crawling January 5th, shell about 0·37 mm. across and still without sculpture. The species can be recognised easily at this stage. Although when newly hatched it is larger than any of the rissoids known, it loses the velum at a smaller size and with fewer whorls than most of the others, having hardly 2½ whorls at metamorphosis (Plate II, Figs. 11–14). Capsules and larvæ were found in their natural surroundings on and near Zostera in spring.

PLATE III.

Rissoa parva, Rissoa guerini, Cingula semistriata, Cingula semicostata.

(Figs. 1, 4–9, 13–15, 18–23 scale A ; 10–12, 16, 17, 24 scale B.)

FIGS. 1–7.—*Rissoa parva.*
(1) egg-capsules laid in bowl, 0·64 mm. across ; (2–4) newly hatched larvæ from eggs, shell 0·13 mm. across ; (5) young just crawling, having lost velum, shell 0·48 mm. high ; (6) foot of same ; (7) apex of adult shell.

FIGS. 8–14.—*Rissoa guerini.*
(8–9) egg-capsule laid in bowl, (8) newly laid with eggs, capsule 0·96 mm. across ; (9) empty capsule showing hole from which the larvæ have emerged, capsule 0·14 mm. across ; (10) newly hatched larva from egg, shell 0·16 mm. across ; (11–12) slightly older veligers, reared from egg ; (13) young shell from red weed, crawling ; (14) half-grown shell.

FIGS. 15–18.—*Cingula semistriata.*
(15) egg-capsules laid in bowl, 0·64 mm. across ; (16–17) newly hatched larva from egg, shell 0·10 mm. across ; (18) apex of adult shell.

FIGS. 19–24.—*Cingula semicostata.*
(19) egg-capsules laid in glass jar, 0·48 mm. across ; (20) young newly hatched, shells 0·30 mm. across ; (21) slightly older shells ; (22) apex af half-grown shell ; (23) apex of adult shell ; (24) young shell much enlarged.

RISSOA PARVA (DA COSTA).

(Plate III, Figs. 1–7).

The commonest of all the rissoids, occurring abundantly between tidemarks and below on all parts of the coast, laying eggs on seaweeds where it lives. Pelseneer (1911) states that its spawn is abundant in spring and summer on red algæ (*Callithamnium*, *Griffithsia*, etc.) on the Brittany coast, capsules about 1 mm. in diameter, transparent and colourless, and contain from 6 to 35 eggs. Near Plymouth it lays eggs on both brown and green weeds, especially in the rock pools exposed at spring tides, where it is present in huge numbers, both the type and the var. *interrupta*. It appears to breed most of the year but chiefly in spring and summer, Veliger is usually to be found in the plankton, attaining 3 to 3½ whorls before losing velum. Specimens in bowls laid eggs on Zostera, December 4th. Capsules similar to those of *R. membranacea* but much smaller and higher in proportion to the width. Diameter 0·64 mm., height 0·30 mm., containing from 20 to 50 eggs, about 0·09 mm. across (Plate III, Fig. 1). All the eggs hatched out in about 10 days. Larva very like *R. membranacea* but smaller, 0·13 mm. across shell when newly hatched (Plate III, Figs. 2–3) with 1½ whorls, colourless, transparent, without sculpture. Velum colourless, about 0·13 mm. across. Eyes, otocysts, mouth and foot well developed but no front process to foot at first. Veliger alters little but grows quickly, foot becoming brownish and later having the dark purplish brown markings at junction with body on each side, velum remaining colourless but growing large, more than twice width of shell; body whorl (third) of late larva with fine line round periphery. Shell now 0·48 mm. long. Animal can now swim or crawl (Plate III, Figs. 5–6). Velum disappears and little Rissoa is like adult except for colouring which begins to be a pale horn-colour and even on third whorl at top of outer aperture on outside is a faint indication of the brown falciform mark separating this species from all others.

RISSOA GUERINI RÉCLUZ.

(Plate III, Figs. 8–14).

Fairly common round Plymouth coast among weeds at extreme low water and below, chiefly off Drake's Island in Sound. One specimen in bowl laid 2 egg-capsules on February 16th on Zostera. Later on the same animal laid several more capsules on the sides of the bowl, through February, March and April. First capsule 0·96 mm. across, 0·16 mm. high (Plate III, Fig. 8), thin-walled, colourless and transparent, containing about 80 eggs, 0·09 mm. across. Some of the later capsules are larger, 1·1 mm. across, with a broad margin making the whole 1·4 mm. (Plate III, Fig. 9). The larvæ escaped in 10 days leaving a large hole at the top of the capsule and swam away as veligers. Larval shell 0·16 mm. across when newly hatched with about 1½ whorls, colourless, transparent, without sculpture; animal and velum also colourless at first, velum 1·2 mm. across (Plate III, Fig. 10). Shell rather more compact than *R. membranacea* and *R. parva*, slightly smaller. In a few days velum becomes characteristically spotted with dark brown (Plate III, Figs. 11, 12), spots also on body, 2 on each of velar lobes, one in centre between eyes, one in centre at base of foot and brown pigment round mouth. Veligers in this stage occur in plankton and also later stages in which colour has increased; foot yellowish brown with dark spots, velum bordered with brown spots more or less irregular. As soon as pigment appears, larva easy to distinguish. Metamorphosis when there are about 3 to 3½ whorls; no pattern on shell until about 5th whorl which suddenly enlarges and has brown spots round periphery (Plate III, Fig. 14).

RISSOA INCONSPICUA ALDER.

(Plate IV, Figs. 13–15.)

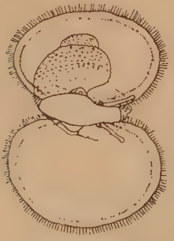
Fairly common on sandy gravel in parts of Sound, and among weeds, close to coast or beyond. Jeffreys (1867) has recorded it as common in trawl refuse at Plymouth but in those days this was brought close inshore, a practice now discontinued. It is still to be found sometimes in trawl waste and later stages just metamorphosed are sometimes in tow-nets from both inside and outside Sound. Most frequent off White Patch, on east of Sound, close to shore, beyond low-water mark. Adults from here laid eggs in bowls on Zostera and also on one another and on pieces of debris. Egg-capsules small, 0·48 mm. to 0·64 mm. across, sometimes smaller, about 0·12 mm. high, clear and colourless, containing about 6–9 eggs, 0·08 mm. across when newly laid. Young hatch as veligers in 10 days; shell smooth, unsculptured, about 0·10 mm. across; velum colourless at first, about 0·10 mm. across; foot, eyes, otocysts and tentacles all present. Velum later bordered with brown; older larvæ with two faint spiral lines round body whorl. These are common in early autumn. Newly metamorphosed shells have the purple apex characteristic of the adult, but there is no sculpture on the first 3 whorls except a slight spiral broken line just above periphery of third whorl.

RISSOA SARSII ALDER.

(Plate I, Figs. 1–16; Plate II, Figs. 1–5.)

Eaten when very small by young herrings (see page 523). Larvæ recognised in egg-capsules from which veligers were hatched. Later

PLATE IV.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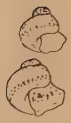
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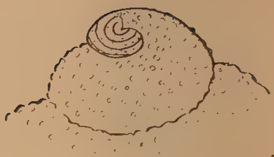
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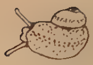
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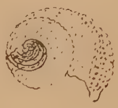
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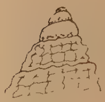
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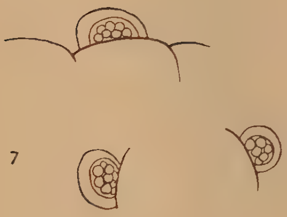
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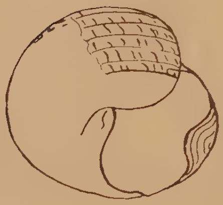
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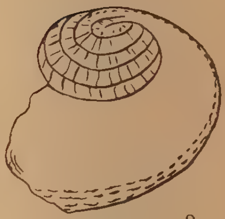
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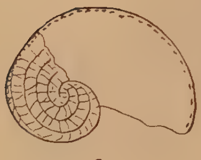
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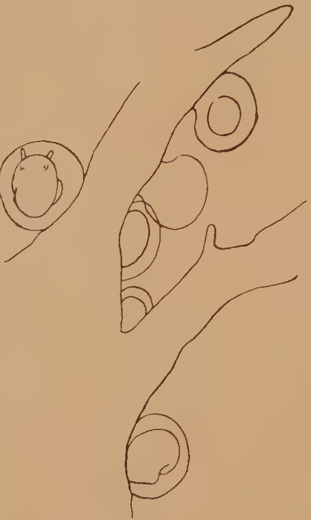
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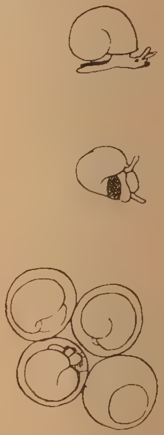
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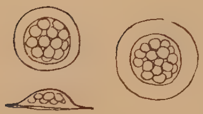
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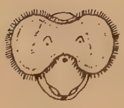
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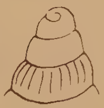
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larvæ from plankton reared in plunger-jars until species was distinguishable. One grew to adult size, several were three-parts grown. Egg-capsule planktonic, not unlike that of *Littorina littorea* but differs in shape, and size. Colourless, transparent and somewhat disc-shaped, it is rather more convex on one surface than on the other, and slightly indented near the margin, 0·18 mm. across, 0·08 mm. high ; contains only one egg, about 0·08 mm. across, situated in the centre of capsule with large space as broad as itself surrounding it (Plate I, Figs. 2–6). Before larva is hatched it shows characteristic sculpture of the shell consisting of longitudinal striations with small dots in between. When hatched shell measures 0·08 mm. across, growing quickly to 0·16 mm. with one and a half whorls after which the spiral sculpture ceases and just above and below periphery a series of dots forms an irregular spiral band leaving upper and under surface smooth except round the incipient umbilicus where are a few dotted striæ (Plate I, Figs. 7–15). Whilst the larva is still very small with hardly more than the whorls having dotted striæ it is eaten by the young herring (Plate I, Fig. 1). Shell colourless and transparent, soon assuming a pale horn-colour, aperture dark brown. Animal and velum typically rissoid in shape. Velum gradually becoming bordered with a fine brown band just inside the outer row of cilia, sometimes absent on one side. Characteristic sculpture easily seen when shell has about 3 or 3½ whorls, measuring 0·48 mm. high. Animal yellowish with a dark mass at origin of foot, purple streak on foot which is bluntly pointed and with a very flexible fore part. Tentacles long and contractile, mantle tentacle and hind tentacle above foot present, the latter very long. Larva is now ready to metamorphose and can both swim and crawl and soon loses velum (Plate I, Figs. 16–21 ; Plate II, Fig. 1). Just before it loses velum it is extremely common in the Plymouth plankton, both inside and outside Sound, especially inside, from early to late spring, hardly any being left in summer. Floating egg-capsules chiefly in late autumn and winter ;

PLATE IV.

Alvania punctura, *Rissoa inconspicua*, unknown rissoid, *Barleeia unifasciata*.

(Figs. 1, 4 scale C ; 2, 3, 6,7, 11–13, 15 scale A ; 5, 8–10 scale B.)

Figs. 1–7.—*Alvania punctura*.
(1, 2, 4) late veligers, shell 0·50 to 0·64 mm. high ; (5) apex of same enlarged ; (3) larva crawling, having lost velum ; (6) apex of adult shell ; (7) egg-capsules laid on shells of neighbours in bowl, capsules 0·32–0·48 mm. across.

Figs. 8–10.—Shells of unknown rissoid larvæ, 0·20 to 0·25 mm. across.

Figs. 11–12.—Egg-capsules and larvæ of *Barleeia unifasciata*, laid in bowl on weed, capsules 0·56 mm. across.

Figs. 13–15.—*Rissoa inconspicua*.
(13) egg capsules laid in bowl, 0·48 to 0·64 mm. across ; (14) Newly hatched larva from egg, shell 0·10 mm. across ; (15) Apex of adult.

young larvæ very abundant in plankton from December to February and March. Late larvæ (Plate II, Figs. 2–5) attained 6 whorls in 4 months, the adult having 7 whorls. Probably they become mature within a year. Older shells usually with brown streaks on fourth whorl running from suture, generally broken at periphery, often a brown line below last whorl, beginning at the sixth, shell sometimes clear brown without streaks. Animal with deep brown opercular lobes, very long light tentacles and processes.

Rissoa sarsii is not very well known. It was described by Lovén in 1864 from specimens found by Sars at Bergen. It is the *Rissoa inconspicua* var. *tenuis* of Forbes and Hanley (Plate LXXXII, Figs. 7–8) and the *Rissoa albella* var. *sarsii* of Jeffreys (1867). Alder found it at Rothesay a little below low-water mark and describes the animal but makes no reference to the long tentacles and posterior process (Forbes and Hanley, 1853). The only specimen reaching the adult stage at Plymouth was a brown variety having streaks only on upper whorls, last whorl with 2 dark bands above and one below periphery. Seven whorls; animal yellowish white, slightly spotted on head with brown; opercular lobes dark brown, tentacles and posterior processes light and very long. Outer lip of this specimen abnormally produced in an outstanding rib. Length 3 mm.

Cingula semistriata (Montagu).

(Plate III, Figs. 15–18.)

A very common rissoid, occurring between tide marks and below, on weeds, hydroids, bryozoa and stones. Laid eggs in bowl on Zostera in June. Similar capsules on weeds through summer. The fixed capsules of typical form but smaller and higher in proportion to diameter than *Rissoa membranacea*, *R. parva* and *R. guerini*, 0·56 mm. to 0·64 mm. across, 0·24 mm. high, colourless and transparent (Plate III, Fig. 15). Eggs usually from 12 to 22, about 0·08 mm. across. Newly hatched larva 0·10 mm. across shell (Plate III, Figs. 16–17) with rather more than one whorl, no sculpture, animal and velum colourless (Plate III, Fig. 16). Later stages only recognised in plankton when nearly ready to metamorphose when there are 2 conspicuous lines below suture as in adult (Plate III, Fig. 18); velum always colourless; 3 processes behind operculum.

Cingula semicostata (Montagu).

(Plate III, Figs. 19–24.)

Very common at Plymouth under stones between tide marks and in muddy gravel among stones further out. Eggs laid singly in jars standing in running water with gravel and small stones, in single capsules, sometimes one or two together adhering to small particles, March to May.

Unlike the usual rissoid capsules this is oval, very tough and thick-walled, 0·48 to 0·64 mm. by 0·32 to 0·48 mm., usually fixed by the centre of one side (Plate III, Fig. 19). Egg enclosed in membrane, 0·24 mm. across when newly laid ; velum formed within capsule and reaching a width of 0·48 mm. ; shell 0·32 mm. across ; eyes and short tentacles present and a lobe in front of eyes ; foot bluntly pointed ; shell faintly but quite perceptibly striated longitudinally, the striæ formed by minute dots, sometimes irregular and rough, velum gradually disappears and before hatching is lost, the animal breaking out of the capsule in the crawling stage (Plate III, Figs. 20, 21). It can easily be recognised by its likeness to the adult and is present with these at various times of year. Both shell and animal creamy white.

ALVANIA PUNCTURA (MONTAGU).

(Plate IV, Figs. 1–7.)

Very common on the outside dredging and trawling grounds, rarely nearer the coast. Obtained alive from trawl and dredging refuse. Larvæ abundant in summer and early autumn in tow-nettings usually from outside. Egg-capsules laid in bowl on the shells of one another, small and thick-walled, 0·32 to 0·48 m.m. across, rather higher than most rissoid capsules but some are typically lens-shaped. Each contains about 12–14 eggs, 0·06 mm. across (Plate IV, Fig. 7). Young from these eggs did not hatch out but minute larvæ, evidently newly hatched, are very common in summer plankton which obviously belong to this species. It is easy to recognise them for they have at first the same sculpture on the apex as *Rissoa sarsii,* but the part striated with spots is smaller than in that species, 0·05 mm. across, and after this there are small raised spots on the whorls giving the shell a peculiar papillate appearance. As the larva grows the velum enlarges but is always colourless, animal yellowish white with a little brown, shell becoming a dark horn-colour. Breadth of velum in last stages more than twice length of shell (Plate IV, Fig. 1). Apical whorls of adult which constitute the larval shell are clearly seen (about 3½) after which the adult sculpture begins (Plate IV, Fig. 6). Larval shell about to metamorphose 0·64 mm. long. Those kept in plunger-jars grew into adults.

BARLEEIA UNIFASCIATA (MONTAGU).

(Plate IV, Figs. 11, 12.)

Exceedingly common on weeds at extreme low tide in rock pools, Wembury, living on Fucus or *Calliplepharis jubata*, often with *Rissoa parva.* Unlike *R. parva* the eggs are laid singly in round capsules on the weed, adhering by only a small portion, and the velum is lost before hatching. Laid egg-capsules in the Laboratory on *Calliplepharis*, May 29th (Plate IV, Fig. 11), 0·56 mm. across, more or less round, egg 0·32 mm. across, develops into pale brown shell turning to dark brown, with small velum which soon disappears and red operculum. Shell 0·42 to 0·48 mm. across with 1½ whorls, smooth and without sculpture, apex very blunt, much blunter than any rissoid known. At this size the animal hatches without a velum and crawls about. Many are to be seen on the weed with adults and young of all sizes. No posterior and no mantle tentacle. Barleeia seems to be further removed from a true Rissoa than any of the other genera now placed in the family.

Several other larvæ which resemble rissoids in shape, and almost certainly belong to this family, are to be seen in the Plymouth plankton but have not yet been identified. Among these is one with a sculptured apex with spiral striæ divided up by lines (Plate IV, Figs. 8–10). After 1½ whorls the sculpture is irregular dot-like markings in a few lines round periphery, animal pale yellowish with large colourless velum. This is so much like *Rissoa sarsii* and *Alvania punctura* that there is probably some relationship. It occurs with the latter usually outside the Sound in summer.

The following species occurring alive near Plymouth have not yet had their eggs and larvæ identified : *Cingula fulgida*, *C. alderi*, *C. cingillus* and *Alvania crassa*, although the adults of all but *C. alderi* are common round our coasts.

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The Eggs and Larvæ of some British Turridæ.

By

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With Plates I–IV.

In a previous paper (Lebour, 1933) the eggs and larvæ of *Philbertia* (*Comarmondia*) *gracilis* were described, showing lens-shaped sessile egg-capsules and a planktonic larva with elaborately sculptured shell and large brightly spotted velum, which remained as a veliger until it had attained several whorls and was of a large size before metamorphosis. Lens-shaped capsules are apparently typical of the group (Jeffreys, 1867, and observations at Plymouth) and finely sculptured embryonic shells with several whorls are already known in many species (Jeffreys, 1867 ; Cossmann, 1895 ; Thiele, 1929). Researches in the Plymouth plankton show that members of this family are common and are some of the largest and most conspicuous gastropod larvæ. They are therefore of considerable economic importance in the sea.

Winckworth (1932) in his recent list of British Marine Mollusca recognises six genera in the Turridæ. Of these four occur at Plymouth : *Hædropleura*, *Lora*, *Mangelia* and *Philbertia*. Lora (*L. rufa*) has only been seen at Plymouth as a dead shell ; Hædropleura (*H. septangularis*) has only been obtained once alive at Plymouth, but three species of Mangelia (*M. attenuata*, *M. nebula* and *M. coarctata*) and six species (all the British species known) of Philbertia occur, some of which are common. Winckworth recognises the sub-genus *Bela* in Mangelia to which both the common species of Mangelia belong (*M. nebula* and *M. coarctata*) and three sub-genera of Philbertia : *Comarmondia*, *Philbertia* and *Teres*. *Philbertia gracilis* belongs to the sub-genus Comarmondia and is fairly common, usually on the outside dredging grounds, alive ; *Philbertia teres* is the only species belonging to the sub-genus Teres and has not yet been obtained alive at Plymouth, dead shells occasionally occurring in the shell gravel of the Eddystone Grounds ; the sub-genus Philbertia contains *Philbertia leufroyi*, *P. purpurea*, *P. asperrima* and *P. linearis*. *Philbertia purpurea* has occasionally been found alive from low water to 5 fathoms (Mar. Biol. Assoc., 1931) ; *P. asperrima* is dredged sometimes in the Sound ; *P. leufroyi* is fairly common in the outside waters and *P. linearis* is the commonest of all, occurring both in the Sound and outside but most commonly near the coast.

The turrids may be divided into two groups by the embryonic shell and these coincide with Hædropleura, Lora and Mangelia on the one hand, which have a smooth apex, and Philbertia on the other, the species of which have a sculptured apex. Hædropleura and Lora are operculated whilst Mangelia and Philbertia have no operculum in the adult, the larva shedding this on metamorphosis.

Sculptured apices in the species of Philbertia are already known as mentioned above, but the existing descriptions are not always altogether accurate, the fossil species frequently being described with the top whorls smooth when in the living form of the same species they are seen to be reticulated. This is not to be wondered at when one realises that the sculpture may wear away very soon. Tiele (1929) describes the top whorls of Philbertia as spirally sculptured when really it is usually reticulated but in a different way from the following embryonic whorls: Comarmondia, however, has minute flecks instead of reticulations on the top whorl. Mr. Dennis Curry has kindly sent me some specimens of turrids from the Barton Beds whose apices are very similar to the recent species *Philbertia linearis*, *P. leufroyi*, *P. purpurea*, *P. asperrima* and *P. teres*, and one which somewhat resembles that of *Mangelia coarctata*. In his book on shells of Port Alfred, South Africa, Colonel Turton (1933) figures and describes as a new species of Trophon (*T. ornatus*, Plate XVIII, Fig. 544) a shell which is almost certainly the young of a turrid of the Philbertia type with a similar sculpture. It is evident that the sculpture of the embryonic whorls of the Philbertias is an ancient character and one which is world-wide in distribution and we have in it a clear guide to the affinities of those shells which possess such markings.

The embryonic whorls of all the turrids show plainly on the adult shells and those of the Philbertias (excluding *P. gracilis*) are so much alike that it is difficult to see any differences at all. On very close examination, however, although the markings are all of the same type, it is seen that the number of embryonic whorls varies slightly with the species, the whorls may be different in breadth, the colour may be different and the quality of the markings may be more or less distinct. Larval shells of this Philbertia type are common in the plankton in spring and summer; only very occasionally in autumn and winter. They occur both in the inshore and outside plankton. Most of them belong to *Philbertia linearis*, but those of *P. leufroyi* can be recognised, and, probably, those belonging to *P. asperrima*. *P. purpurea* and *P. teres* have not been seen as larval forms. In all the Philbertias the embryonic shell is brown or more or less a dark horn-colour. The following is the sculpture in all the typical Philbertias, e.g. *P. linearis*, *P. leufroyi*, *P. asperrima* and *P. purpurea ;*

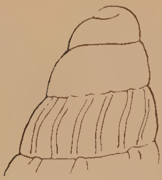
also of *P. teres* : the first whorl or whorl and a half is reticulated (Plate III, Fig. 2), the reticulations being formed by raised spiral striæ and straight striae crossing them at right angles, the points where the striæ meet appearing as slight prominences ; the reticulations are thus straight up and down. Suddenly at about the second half of the second whorl the sculpture changes, a series of raised lines running out from the suture and from there oblique reticulations originate ; as Jeffreys puts it, " like the meshes of a fire-guard " (Plate III, Fig. 3). Here again, where the meshes cross there are raised points. The reticulations are now oblique instead of straight, and they run nearly to the base of the shell where spiral striæ are seen. The third and fourth whorls are carinated and the fifth also in those species which possess more than four embryonic whorls. Below the periphery the reticulations are not so regular, but spiral lines with flecks and smaller reticulations take their place (Plate III, Figs. 6–7 ; Plate IV, Fig. 1). On the last embryonic whorl, third, fourth or fifth, as the case may be, there are three spiral ridges forming the carinations which end in a broad rounded process curving inwards on the outside of the shell aperture and supporting the velum (Plate IV, Figs. 2–3). *Philbertia teres* has the longest embryonic shell (Plate IV, Fig. 11), consisting of 5 to 5½ whorls ; *P. linearis* and *P. asperrima* coming next (Plate IV, Figs. 7, 9) with 4 to 4½ whorls ; *P. leufroyi* (Plate IV, Fig. 8) with 3½ ; *P. purpurea* (Plate IV, Fig. 10) with 3. The embryonic sculpture ends with the loss of the velum, the shell afterwards taking on the adult pattern and losing the operculum (Plate IV, Figs. 4, 5). The animal in all the larvæ known is almost or completely colourless, very rarely with grey or pinkish in parts. The velum is spotted with orange in *Mangelia nebula* and *Philbertia gracilis*, but in all the true Philbertias known it is colourless. At first bilobed, the velum may grow to a large size and in the older larvæ has four lobes, in *Mangelia nebula* being capable of covering both shell and animal like a true veil ; in *Philbertia gracilis* the lobes are very long and narrow, and in the Philbertias proper they are large and broad. Two more larvæ have been seen in the Plymouth plankton which have not yet been attributed to any species. It is very probable that they belong to the smooth-topped turrids. Both have a large and conspicuous velum, with brown or orange colouring.

DESCRIPTION OF THE EGGS AND LARVÆ OF THE PLYMOUTH PLANKTONIC FORMS.

Family **TURRIDÆ**.

The eggs and larvæ have been seen at Plymouth in *Mangelia nebula*, *Philbertia gracilis* and *Philbertia linearis ;* the larvæ hatched out from the egg in the first and second and the later larvæ from the plankton

PLATE I.



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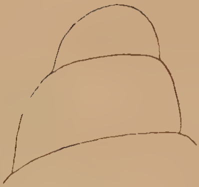

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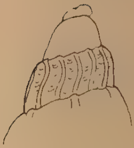

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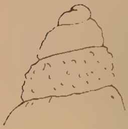

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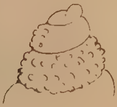

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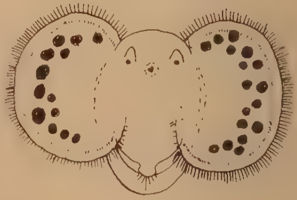

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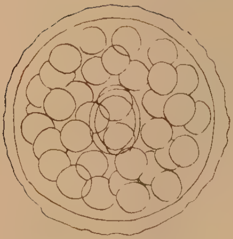

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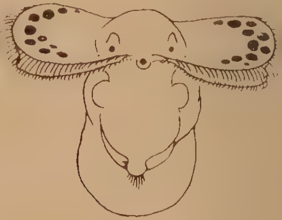

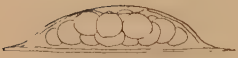

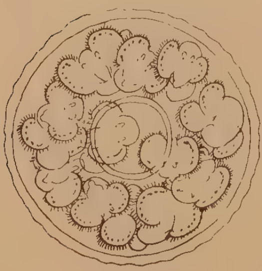

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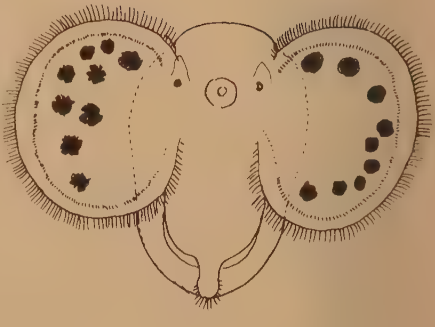

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in all three were reared until metamorphosis. The life-history of *Philbertia gracilis* has already been described (Lebour, 1933), those of *Mangelia nebula* and *Philbertia linearis* are described here for the first time. The eggs of the other species are not known, but the larvæ of *Philbertia leufroyi* and *P. asperrima* have been recognised in the plankton. The two last are so like those of *P. linearis* that a separate description is unnecessary.

In order to obtain the eggs the adults were kept in plunger-jars. It was difficult at first to keep them alive for long because the natural food was not known. The radula which consists of few long pointed teeth suggests carnivores of a predatory type. Most of the species naturally live on shelly or sandy gravel where numerous worms or foraminifera abound. Apparently they do not eat the latter which lived and multiplied quite happily in the same aquarium as the turrids, but it seems very likely that they eat small worms, for the one specimen of *Hædropleura septangularis* and several *Philbertia linearis* have lived for some months in a plunger-jar with brown deposits of some alga which harbours small worms and infusoria in abundance.

Genus Hædropleura.

Hædropleura septangularis (Montagu), (Plate I, Fig. 1). Only one specimen has been seen alive from Plymouth, dredged in the Sound. Apex smooth for 2½ whorls, the third whorl with fairly close ribs. Eggs and larvæ not known.

Genus Lora.

Lora rufa v. *ulideana* (Thompson), (Plate I, Fig. 2), dead shell only, found in outside dredgings, Eddystone Grounds. Smooth rounded apex,

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EXPLANATION OF PLATES.

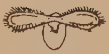
(Scale B is 3 times the scale of A.)

PLATE I.

(Figs. 1–7 scale A, 8–9 scale B.)

Fig. 1.—Apex of adult *Hædropleura septangularis*
Fig. 2.—Apex of adult *Lora rufa*.
Fig. 3.—Apex of adult *Mangelia nebula*.
Fig. 4.—Apex of half-grown *Mangelia nebula*.
Fig. 5.—Apex of adult *Mangelia coarctata*.
Fig. 6.—Egg-capsules of *Mangelia nebula* laid in plunger-jar, 1·6 mm. across.
Fig. 7.—Egg-capsules of *Mangelia nebula* laid on siphon of Lutraria, 1·76 mm. across.
Fig. 8.—Newly hatched larvæ of *Mangelia nebula* from eggs in plunger-jar, shell 0·23 mm. across.
Fig. 9.—Newly hatched larva of *Mangelia nebula* from egg-capsule on *Lutraria* siphon, shell 0·30 mm. across.

PLATE II.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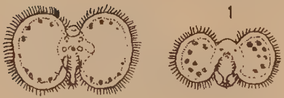
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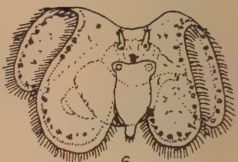
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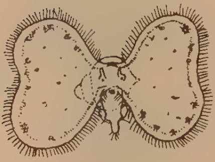
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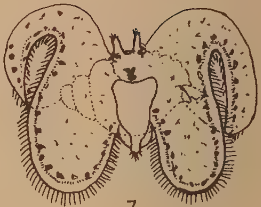
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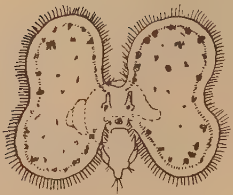
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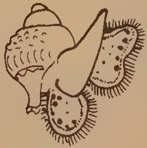
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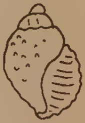
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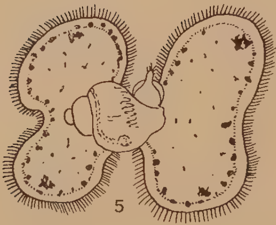
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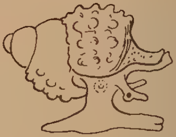
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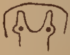
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very broad, of about 2 whorls, the extreme top hidden. Eggs and larvæ not known.

Genus MANGELIA.

Mangelia attenuata (Montagu). Although this species is recorded from Plymouth in the Fauna List it has not been seen recently.

Sub-genus **BELA**.

Mangelia coarctata (Forbes). (Plate I, Fig. 5).

This species occurs in the Sound, off Drake's Island, dredged in sandy gravel and is not uncommon. The first 2½ whorls are smooth, the third with close ribs with striæ in between. Eggs and larvæ not known.

Mangelia nebula (Montagu), (Plate I, Figs. 3, 4, 6–9 ; Plate II, Figs. 1–11).

This species is recorded only from one locality in the Plymouth Fauna list but it is in reality very common and frequently dredged in the Sound, especially in Cawsand Bay and off the White Patch, on the east side of the Sound. More rarely it is found further out. The adult which is a reddish brown colour has a smooth apex, at about the third whorl tending to be tuberculated (Plate I, Figs. 3–4), after which the adult sculpture begins. An adult kept in a plunger-jar laid one egg-capsule, the only one after repeated attempts at keeping the animals which lived for some time in various plunger-jars but never laid any more eggs. Mr. G. A. Steven, however, found some eggs on the dredged severed siphon of a lamellibranch, probably Lutraria, which agreed with those obtained from the mollusc itself in the plunger-jar, and the young which were hatched out were similar. The only difference was in the size, the capsules on Lutraria being larger and the newly hatched larvæ also larger. The larvæ are so peculiar and characteristic that there can be no doubt that they both belong to *Mangelia nebula*. Later larvæ in the plankton were identified as the same mollusc and by keeping these until metamorphosis it was proved that they were *Mangelia nebula*.

PLATE II.

(Scale A) *Mangelia nebula*.

FIG. 1.—Newly hatched larvæ from *Lutraria* siphon.

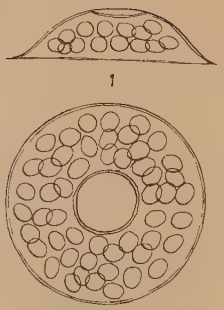
FIG. 2.—The same, 2 days old.

FIGS. 3–9.—Larvæ from plankton.
(3) shell 0·46 mm. long ; (4) shell 0·76 mm. long ; (5) shell 0·80 mm. long ; (6) shell 0·90 mm. long ; (7) shell 0·96 mm. long ; (8) shell 0·90 mm. long ; beginning to lose velum ; (9) empty shell.

FIG. 10.—Metamorphosed larva, shell 1·12 mm. long.

FIG. 11.—Front of same.

PLATE III.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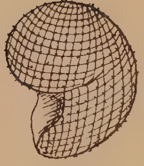
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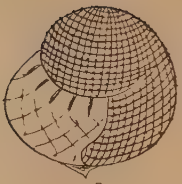
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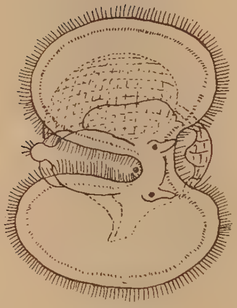
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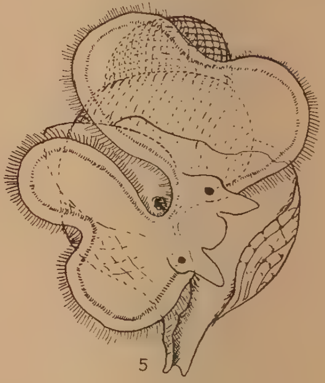
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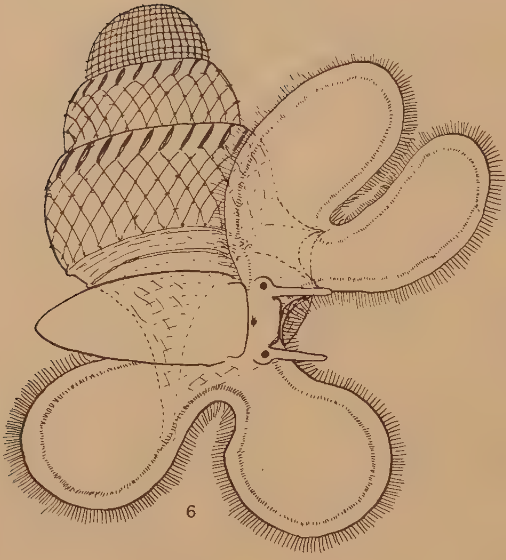
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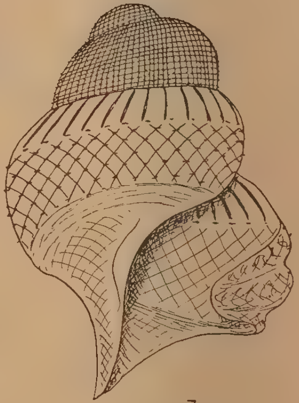
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The egg-capsules (Plate I, Fig. 6) are smooth and transparent, lens-shaped and attached by the under flat surface, the upper surface rounded with a thin part in the centre where a hole is formed when the larvæ are ready to emerge. Diameter of capsule laid in plunger-jar, 30.1.33, 1·6 mm., height 0·32 mm. ; diameter of capsules laid on Lutraria siphon, 18.5.31, 1·76 mm. The eggs when newly laid measured about 0·16 mm. across. There were about 60 opaque eggs in the capsule laid in the plunger-jar ; fewer in those from the siphon which were further advanced (Plate I, Fig. 7). Later on (14.2.33) the larvæ nearly ready to hatch were dying in the capsule and were removed to a fresh plunger-jar in which several veligers hatched out but did not grow and soon died. The newly hatched larva (Plate I, Figs. 8–9 ; Plate II, Fig. 1) is very peculiar. The shell measures about 0·23 mm. across in those from the eggs laid in the plunger-jar ; the foot is short with a rounded ciliated lobe behind ; in front of the eyes is a rounded prominence ; the tentacles short. The velum is bilobed, having large rounded lobes with the usual cilia and measuring 0·4 mm. across or more, ornamented on each side with several large and conspicuous brilliant orange spots. The spots may vary in number and arrangement, about 9 to 12 being usual. Those hatched from the siphon of Lutraria were larger, the shell about 0·3 mm. across and the velum about 0·64 mm. across, but the larvæ were in other respects exactly alike. Those from the siphon lived for a few days and grew, showing a posterior siphon on the shell and the posterior knob of the foot long (Plate II, Fig. 2). Young larvæ were found in the plankton slightly older than this and through the spring and summer later larvæ were common in the tow-nettings both in the Sound and outside, but especially rather close to the coast. The largest numbers occurred from May to September, but specimens were seen also in early autumn. Very young metamorphosed forms were dredged in October and November. As the larva grows the spots on the velum increase and tend to form a border, but they are also irregularly scattered on the surface and sometimes the pigment congregates as a mass at the outer corner of each lobe. The shell is clear, transparent and colourless for about three whorls when it measures about 0·70 mm. in length, the apex slightly oblique, the posterior canal conspicuous ; eyes and tentacles well developed ; foot with three ciliated

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PLATE III.

(Fig. 1 scale A, Figs. 2–7 scale B.)

Fig. 1.—Eggs of *Philbertia linearis* laid in plunger-jar, 1·5 mm. across.

Figs. 2.—Very young larval shell of *Philbertia linearis* from plankton, 0·19 mm. across.

Fig. 3.—Shell of *Philbertia linearis* slightly older, from plankton.

Figs. 4–6.—Later veligers of *Philbertia linearis* from plankton.

Fig. 7.—Shell of *Philbertia leufroyi*, late larva, from plankton.

lobes posteriorly, the median lobe long and projecting beyond the foot. As the animal grows the front of the foot grows beyond the mouth. The velum tends to be four-lobed and grows very large, the breadth being more than three times the length of the shell and in the later stages being held over the shell and animal so that they are completely covered. Thus it swims covered over with a true veil. The shell 0·96 to 1 mm. long, has now 3½ to 4 whorls and the animal is nearly ready to metamorphose. The shell and animal siphon are conspicuous, the eyes on short tentacles showing the adult form, the foot with the lobes dwindling and finally absent. The fourth whorl is now showing a tuberculated appearance, or even the third whorl may show this (Plate II, Figs. 7–9). Near the aperture there may be spiral striæ. The velum then dwindles, the operculum is shed and the animal crawls (Plate I, Fig. 10), becoming like a miniature adult. The front of the foot is almost square, the base a light grey, otherwise the animal is colourless. It is quite easy to recognise all these stages including the young crawling mollusc.

Genus PHILBERTIA.

Sub-genus **COMARMONDIA.**

Philbertia gracilis (Montagu). (Plate IV, Fig. 6).

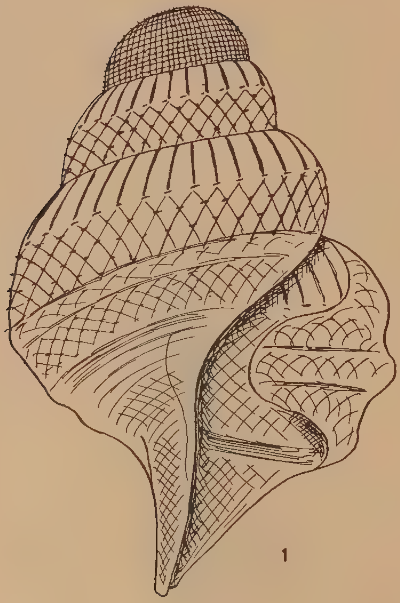
The egg-capsule and larvæ of this species have already been described. Egg-capsules lens-shaped with reticulations on the upper surface. In 1933 a further supply of egg-capsules was obtained in a plunger-jar, April–March, and the larvæ hatched out more successfully. These showed that all the larvæ developed and hatched in a very late stage of development with a long shell siphon and deeply coloured velum. It is thus abnormal for any to be eaten by the others and it is not a case of "nurse" eggs as was at first thought. The top whorls are flecked but not spirally striated and the later whorls conspicuously keeled and marked with oblique striæ. The larva grows to a large size in the plankton, the later stages having four very long velar lobes with orange spots. Both shell sculpture and velum are quite unlike the true Philbertias. The sub-genus should probably be raised to a genus.

Sub-genus **PHILBERTIA.**

Philbertia linearis (Montagu), (Plate III, Figs. 1–6 ; Plate IV, Figs. 3, 5, 7).

Jeffreys has described the egg-capsules and newly hatched larvæ of this species (as *Defrancia*), but the measurement of the capsule and number of eggs do not agree with the Plymouth specimen. He has also noticed the sculpture on the newly hatched larval shell. *Philbertia linearis* is fairly common in dredgings from the Sound and occasionally occurs on the outside grounds on sandy or shelly gravel or in hard-branched Bryozoa. The larvæ are common in the plankton both inside and outside the Sound, but particularly near the coast, in spring and summer, rarely in autumn. Egg-capsules were laid in a plunger-jar in February, 1932, and through March, but the larvæ died before hatching although moving about and possessing a shell and velum. A single capsule was laid by another individual in January, 1933. The capsules of the first lot measured 1·5 mm. across, the second measured 2 mm. The capsules described by Jeffreys measured ⅕ inch across and contained 200 to 300 eggs whilst the eggs in the first lot from Plymouth numbered only about 60 and in the second lot about 80. It is possible that there was some mistake in Jeffreys' species. The Plymouth eggs measured 0·14 mm. to 0·15 mm. across The egg-capsule (Plate III, Fig. 1) is lens-shaped, like that of *Mangelia nebula*, and has no reticulations similar to *Philbertia gracilis*. It is colourless and transparent. Very young larvæ were found in the plankton and also all stages up to the latest larvæ which metamorphosed into *Philbertia linearis*. The earliest free-swimming larvæ (Plate III, Fig. 2) were seen in February and various stages were found throughout the spring and summer, dwindling in early autumn and absent in December and January. All the larvæ, even those quite newly hatched, have a dark brown shell with conspicuous straight reticulations, as described above. The velum is colourless, at first bilobed, then larger and slightly indented at the sides to form four blunt lobes. It has the usual cilia round the edge. Eyes and tentacles conspicuous. The rest of the animal is colourless, the foot at first short with a small knob posteriorly ; round thin operculum ; mouth showing in front ; later the foot is pointed behind and the front part covers the mouth. The youngest larva seen measures about 0·19 mm. across the shell and has one whorl and a half ; the outer lip produced for support of the velum. Very soon the oblique striations begin and the shell canal is formed (Plate III, Fig. 3). Later, the shell being about 0·44 mm. long with a conspicuous canal, there are 2½ whorls and the velum is beginning to be four-lobed (Plate III, Fig. 5). The foot at this stage is bluntly pointed and the tentacles well developed. When the shell is about 0·52 to 0·80 mm. long there are 3½ to 4 whorls, the velum is much larger and may project some way beyond the shell, the siphon projects from the shell siphon and the foot is like the adult. It is now nearly ready to metamorphose and when the shell has 4½ whorls and measures about 0·96 mm. the animal can crawl as well as swim and very soon loses the velum and operculum, and the adult sculpture begins. This species must remain a long time as a veliger and is one of the common forms in the Plymouth plankton.

PLATE IV.



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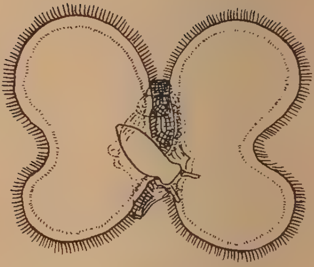

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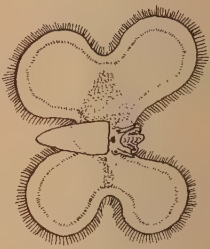

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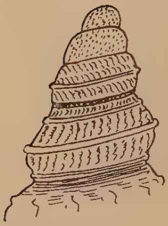

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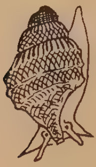

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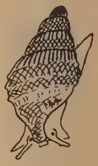

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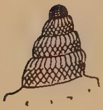

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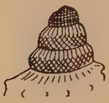

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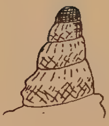

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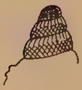

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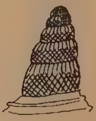

11

Philbertia leufroyi (Smith), (Plate III, Fig. 7, Plate IV, Figs. 2, 4, 8).

Although the species is not recorded in the Plymouth Fauna list it is not uncommon in the outside dredging grounds and has probably been confused with *P. linearis* which it closely resembles. It is, however, broader and larger and more speckled with brown instead of having brown lines. The apex is very like that of *P. linearis* but with fewer whorls (Plate IV, Fig. 8) and broader, therefore by measurement the larval shells may be distinguished and as the veliger has fewer whorls for its size than *P. linearis* it may be distinguished in the later stages. The velum in the late stage is larger than in *P. linearis*, but the animals are very similar. There are 3½ whorls in the embryonic shell of *P. leufroyi* and they may be of a pinkish brown to deeper brown. Jeffreys has noticed the reticulations on the whorls. No egg-capsules were seen, but the breeding season appears to be in spring and summer and the larvæ are seen together with those of *P. linearis* or separate.

Philbertia asperrima (Brown), (Plate IV, Fig. 9).

Jeffreys noticed the sculpture on the embryonic whorls of this species. It is occasionally dredged in the Sound and outside but is not common. The larvæ are very like those of *P. linearis* and *P. leufroyi*, the animal being slightly grey on the body and foot. There are 4½ whorls as in *P. linearis* but the spire is rather longer and the markings are much more irregular, the colour being lighter. These larvæ are not at all common and are very difficult to distinguish from *P. linearis*. They occur in summer. No egg-capsules have been found.

PLATE IV.

(Fig. 1 scale B, Figs. 2–11 scale A.)

Fig. 1.—Late larval shell of *Philbertia leufroyi*, nearly ready to metamorphose, from plankton.

Fig. 2.—Late veliger of *Philbertia leufroyi*, just before metamorphosis, from plankton.

Fig. 3.—Late veliger ef *Philbertia linearis* not quite ready to metamorphose, from plankton.

Fig. 4.—*Philbertia leufroyi*, metamorphosed in plunger-jar.

Fig. 5.—*Philbertia linearis* metamorphosed in plunger-jar.

Fig. 6.—Apex of adult *Philbertia gracilis*.

Fig. 7.—Apex of adult *Philbertia linearis*.

Fig. 8.—Apex of adult *Philbertia leufroyi*.

Fig. 9.—Apex of adult *Philbertia asperrima*.

Fig. 10.—Apex of adult *Philbertia purpurea*.

Fig. 11.—Apex of adult *Philbertia teres*.

Philbertia purpurea (Montagu), (Plate IV, Fig. 10).

Jeffreys noticed the sculpture on the embryonic whorls. It is recorded from several localities in the Plymouth Fauna list but is seldom found, and only one dead specimen from the Eddystone sandy gravel has been seen in recent years. The embryonic shell has only 3 whorls, the smallest number of all the Plymouth species, but the same sculpture as the other Philbertias is present. The eggs and larvæ have not been seen.

Sub-genus **Teres**.

Philbertia teres (Reeve), (Plate IV, Fig. 11).

Jeffreys noticed the sculpture of the embryonic whorls of this species. It has not before been recorded from Plymouth and has only been seen as dead specimen from the Eddystone shell gravel. It has the typical Philbertia sculpture but the adult shell has spiral ribs on the adult whorls. This species has the largest number of embryonic whorls of any of the Plymouth Philbertias and is already know to have such a long apex, consisting of 4 or 5 whorls, 5 in the Plymouth specimen, 4 according to Thiele (1929). The eggs and larvæ are not known.

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On the Occurrence of the Siphonophores *Muggiæa atlantica* Cunningham and *Muggiæa kochi* (Will) in the English Channel.

By

F. S. Russell,
Naturalist at the Plymouth Laboratory.

In 1892 Cunningham described a new species of Siphonophore, *Muggiæa atlantica,* which was first noticed by him in the waters of the English Channel off Plymouth in the autumn of 1891. Since then there have been records from time to time of the occurrence of this species at Plymouth (see Plymouth Marine Fauna, 1931, p. 84), and its distribution in the English Channel and Irish Sea in 1904 was worked out by Gough (1905).

While examining a number of Muggiæa caught off Plymouth in the autumn of 1933 I noticed that the species differed slightly from Cunningham's description. On closer examination it was found that the species was *Muggiæa kochi* (Will) which although superficially resembling *M. atlantica* differs mainly in that the hydrœcium is shorter and the somatocyst only extends to between a third and a half the height of the nectosac. On examining large numbers of specimens it was found that in 1933 no *M. atlantica* occurred in the catches of plankton but all were *M. kochi.* It was of interest therefore to know whether *M. kochi* had appeared in the waters of the English Channel in previous years with *M. atlantica.* Opportunity for such an examination was afforded by the storage in the Plymouth laboratory of all the fortnightly catches taken from the Seven Stones Light-vessel since the year 1913. This collecting was stopped at the end of 1928, but in later years the data have been supplemented by the examination of weekly hauls taken with a 2-metre stramin ring-trawl 2 miles east of the Eddystone. Examination of all these collections has given the following interesting information (see page 556) on the occurrence of the two species.

From the data supplied it seems that *Muggiæa atlantica* occurred for an unbroken series of years from 1913 to 1924 (excepting 1915, when none were seen in the collections), but that in 1925 *M. kochi* first made its appearance and that since that time *M. atlantica* has disappeared from the area.

	M. atlantica.	*M. kochi.*
	Seven Stones.	
Aug. 5th, 1913	+	—
Nov. 1st ,,	+	—
Dec. 14th ,,	+	—
Jan. 28th, 1914	+	—
June 25th ,,	many	—
Aug. 24th ,,	+	—
July 2nd, 1916	many	—
Sept. 30th ,,	many	—
Aug. 5th, 1917	+	—
May 11th, 1918	+	—
Sept. 11th, 1919	+	—
Oct. 16th ,,	many	—
Oct. 28th ,,	+	—
Aug. 2nd, 1920	+	—
Oct. 27th ,,	+	—
Nov. 8th ,,	+	—
July 11th, 1921	+(1)	—
July 22nd ,,	+	—
Aug. 7th ,,	many	—
Sept. 6th ,,	many	—
Sept. 20th ,,	+	—
Oct. 26th ,,	many	—
Nov. 7th ,,	many	—
Dec. 1st, 1921	many	—
Dec. 14th ,,	+	—
Aug. 6th, 1922	many	—
Aug. 31st, 1923	+	—
Nov. 1st ,,	+	—
Nov. 12th ,,	+	—
Dec. 2nd, 1924	+	—
Oct. 4th, 1925	—	+(1)
Oct. 17th ,,	—	+(1)
Oct. 22nd, 1926	—	+
Jan. 4th, 1927	—	+(1)
Sept. 15th, 1928	—	+(1)
Sept. 30th ,,	—	+
	Plymouth.	
Oct., 1928	—	+
Aug.–Dec., 1930	—	+
Jan.–April, 1931	—	+
Aug. 28th ,,	—	+(1)
Oct.–Dec. ,,	—	+
Aug.–Dec., 1933	—	+
Jan.–Feb., 1934	—	+

+ = present.
— = absent.
(1) = only one individual in the catch.

There are no records for 1929. In 1932, although collections were exam-examined weekly, no Muggiæa were found. Unfortunately I discovered the disappearance of *M. atlantica* after I published my report (1933) on the seasonal distribution of the ring-trawl plankton and in Table I in that publication the Muggiæa occurring in 1930–1931 are given as *M. atlantica.* These specimens have been re-examined and found to be *M. kochi.*

Both species are warm water forms and it is remarkable that they have not appeared together in some years or even alternated from year to year. One would like to have information from other regions to see if *M. kochi* now predominates in its area of distribution. The two species were at any rate present together in 1931, for I understand from Mr. A. K. Totton of the British Museum that he took both *M. atlantica* and *M. kochi* in the Bay of Algeciras. The actual geographical distribution of both species appears to be little known and they seem to have been rarely met with in the collections of oceanographical expeditions. Moser (1925, p. 107) remarks that *M. atlantica* has not been taken in the Atlantic outside British waters, but has been found twice in the Pacific, by Doflein in Sagami Bay on the Japanese coast and by Bigelow in the eastern tropical Pacific. More recently it has been recorded by Bigelow and Leslie (1930) as frequent in the plankton of Monterey Bay on the Californian coast of America. It is remarkable, however, that Bigelow (1911) did not find this species in the Biscayan plankton collected by Fowler on the *Research*, nor was the species recorded in the collections of the Plankton Expedition (Chun, 1897). That it probably does occur in the Atlantic outside British waters is, however, suggested by the statement of Totton quoted above.

Moser states on the other hand that *M. kochi* is very frequent not only in the Mediterranean but also in the whole central Atlantic, being recorded by Chun near the Canaries, Fewkes on the coast of N. Carolina and by herself in material collected by Hartmeyer from the Tortugas. Until now, Bigelow's record (1911) from the Bay of Biscay was the most northerly record for its occurrence.

It seems possible that both species are essentially inhabitants of less contaminated coastal waters, which would account for their absence in the collections of oceanographical expeditions. When occurring in our waters they generally first appear towards the end of the summer and often continue on through the autumn to the January or February in the following year.

A number of *M. kochi* were measured from the catches on October 25th and November 15th, 1933. These specimens had been preserved in formalin.

Overall measurements from the mouth of the nectosac to the exterior apex varied between 2·3 mm. and 4·9 mm., the majority lying between about 2·7 and 4·0 mm. Measurements of the distances between the mouth of the nectosac and the summits of the somatocyst and of the hydrœcium showed that on the average the somatocyst extended 51–52% of the height of the nectosac from its mouth, and the hydrœcium 15–16%, the range for the former being 41–59% (1 extreme measurement gave 68%) and for the latter 13–19%.

I am very grateful to Mr. A. K. Totton for kindly confirming the identification of many specimens of the two species.

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Variations in the Amount of Macroplankton by Day and Night.

By

A. C. Gardiner, M.A.

With 3 Figures in the Text.

THE investigations of the International Passamaquoddy Fisheries Commission were concerned, *inter alia*, with the principal food fishes of the region, one of which was the Herring. Demarcation of the spawning areas necessitated a study of the geographical distribution of the larvæ, for which purpose a modified Petersen's Young Fish Trawl was employed. My thanks are due to Mr. Michael Graham, to whom I am greatly indebted for the opportunity of examining the interesting collections of macroplankton on which this account is based.

My thanks are also due to Doctor C. J. Fish for his assistance, to Professor W. M. Tattersall for his help in the identification of the Euphausiids and to Professor Alexander Meek for confirmation of the Sagitta present in the material.

The collections covered a period of 48 consecutive hours, during the course of which 20 oblique hauls, from bottom to surface, were made with a stramin ring-trawl 5 feet in diameter. The net was fitted with two bridles only, a sinker being attached to the lower edge of the ring by means of a strop 6 feet long. The method of fishing was the same as that employed in an earlier experiment (Gardiner and Graham, 1925, p. 3), but with the additional precaution that the angle of the towing warp was kept at 35° to 45°. As before, each haul was of 30 minutes duration.

The times at which the hauls were made are given in Table I, and the approximate course of the boat, drifting under the influence of wind and tide, is shown in Figure 1. The twenty Stations were centred on the position 43° 50′ N. by 64° 30′ W., roughly 17 miles off Liverpool, Nova Scotia. Observations were continued from 8.42 p.m. on May 9th to 6 p.m. on May 11th, 1932. The wind was variable and light, and the sea, save at the first Station, comparatively smooth (0–3 Beaufort). With one exception, Station N. 234, when there was a haze, the sky was clear. Surface temperature ranged from 4·4° to 6·8° C.

The common species in the collections were :—

Thysanoëssa raschii M. Sars.	*Sagitta elegans* Verrill.
,, *inermis* Kröyer.	*Calanus finmarchicus* (Gunnerus).
,, *longicaudata* Kröyer.	*Calanus hyperboreus* Kröyer.

Specimens of *Themisto compressa* Goës, f. *compressa* Goës (Stephensen), *Metridia longa* (Lubbock) and *Pareuchæta norvegica* (Boëck) occurred in many of the collections in addition to occasional small hauls of Decapod larvæ and Cœlenterates. In the first haul, N. 217, the net touched bottom and this collection contained some 250 specimens of *Erythrops erythrophthalma* (Goës).

The numbers of the more abundant species taken in each of the 20 oblique hauls are given in Table I.

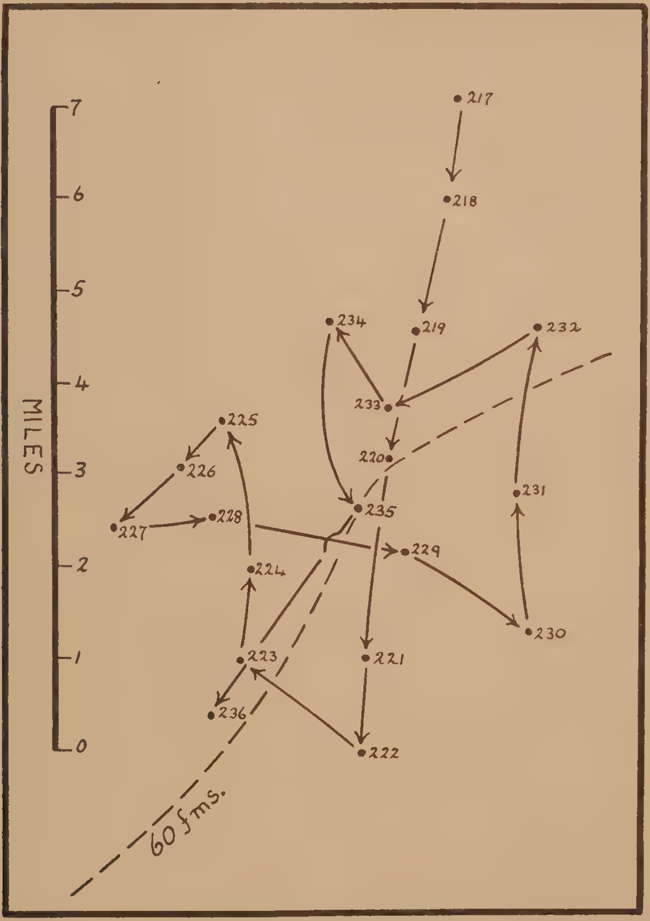
TABLE I.

NUMBERS OF SELECTED ORGANISMS IN EACH OF THE TWENTY COLLECTIONS, MAY 9–11TH, 1932.

Station.	Soundings in Fathoms	Time (A.S.T.).	*Th. raschii.*	*Th. inermis.*	*Th. longicaudata.*	*S. elegans.*	*C. finmarchicus.*	*C. hyperboreus.*	Herring Larvæ.	Fish Ova.
N. 217	56	2024	3,018	49	0	5,750	3,250	1,550	22	147
218	50	2206	3,210	350	0	6,100	1,100	275	29	260
219	51	0004	5,232	80	0	12,880	3,120	1,200	25	432
220	55	0151	2,886	240	0	10,800	4,800	1,440	12	438
221	65	0347	1,281	427	28	4,500	6,450	2,950	0	130
222	72	0628	59	59	2	2,475	6,050	1,400	1	244
223	56	0916	3	0	0	1,020	3,480	760	0	297
224	42	1214	0	0	0	1,180	1,380	520	1	305
225	45	1531	1	0	0	1,550	4,000	1,750	2	190
226	50	1819	6	0	0	2,375	3,750	1,250	5	365
227	50	2010	1,276	36	17	2,750	3,575	850	2	201
228	56	2214	2,427	218	0	3,300	10,200	3,400	0	137
229	65	0008	3,310	814	55	3,720	13,200	1,680	3	180
230	65	0144	3,147	725	0	7,350	11,600	5,500	2	164
231	64	0342	2,278	362	0	9,675	5,650	6,450	1	176
232	58	0623	33	12	1	2,550	6,300	5,800	0	64
233	58	0855	27	2	0	2,975	4,200	1,100	8	85
234	55	1148	7	13	0	1,175	3,250	1,450	5	121
235	60	1529	5	0	0	3,550	4,600	1,750	0	397
236	48	1809	10	2	0	2,925	2,525	675	2	445

The data are expressed graphically in Figures 2 and 3. The curve for Euphausiids is based on the totals of the three species.

As far as the Euphausiids are concerned, virtually none was taken in the daytime, and no statistical treatment need be invoked to demonstrate a significant difference. Sagitta, too, showed a marked discrepancy between day and night hauls, the latter comprising 75% of the total catch. In the cases of *Calanus finmarchicus* and *C. hyperboreus* 61% of the total numbers of each of these species were taken in the night collections. These differences can be shown to be significant, and are not to be ascribed to the operation of chance in irregularly distributed populations.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60 fms.

FIG. 1.—Approximate positions of Stations, and course of vessel drifting under influence of wind and tide.

No such difference exists in the case of the Fish Ova. The catches of Herring larvæ on the first night (Stations N. 217 to N. 220) were undoubtedly in excess of those made during the ensuing daylight period. At first sight this would seem to be in accordance with Russell's findings for Clupeid larvæ (Russell, 1930, p. 649), but the results of the second night's observations coupled with a study of the positions at which the

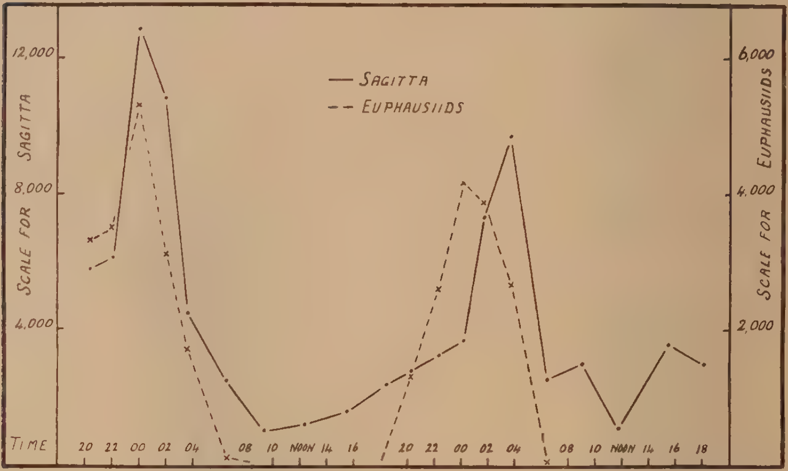

Fig. 2.—Actual numbers of Euphausiids and of Sagitta occurring in each of the twenty collections.

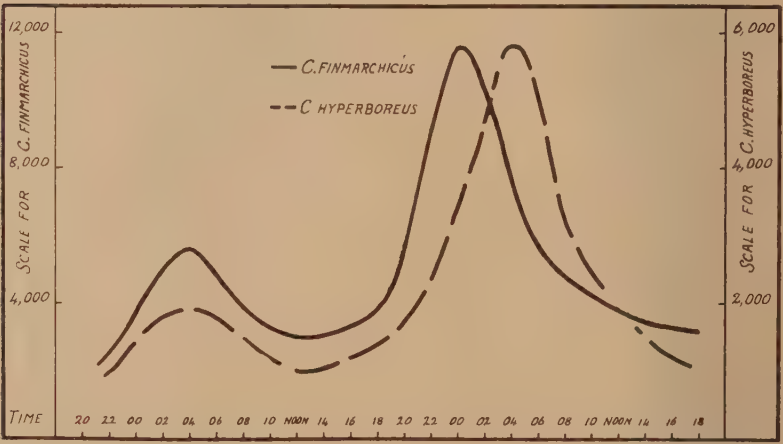

Fig. 3.—Abundance of *Calanus finmarchicus* and of *C. hyperboreus* throughout the period of 48 hours covered by the observations.

bigger catches occur would suggest that the larvæ were restricted to a definite area (see Fig. 1, p. 561).

It has been shown in an earlier paper (Gardiner and Graham, 1925, p. 6) that consecutive hauls of a Petersen's Young Fish Trawl will not catch each time the same number of organisms, and it appeared that fluctuations in the region of ±40% were to be expected. The conclusion arrived at was that the greater part of such differences was due to irregularity in the horizontal distribution of the organisms themselves, a view which has been confirmed by more recent work (see Gardiner, 1931, p. 453). In these circumstances, then, one is clearly entitled to smooth the curves, especially since the purpose of the diagrams is to represent differences which, as already stated, are significant. Smoothing has been carried out in the cases of *C. finmarchicus* and *C. hyperboreus* only, the greater degree of uniformity in horizontal distribution rendering this unnecessary for the Euphausiids and for Sagitta.

Larger catches by night than in the adjacent hours of daylight have been recorded by a number of workers for many planktonic animals ; the reverse has also been observed. So far as can be ascertained it is usually held that in the former case such differences result from a proportion of the animals moving to depths greater than have been (or can be) fished by the net. In the case of some species, especially larger and more active ones, it has also been suggested that discrepancies may result from the animals' ability to dodge the net. In the present instance we have three classes of animals, differing in size and swimming power, all of which have been caught in greater numbers in the darkness, thus enabling these two suggested explanations to be examined.

EUPHAUSIIDS

There is abundant evidence from the literature that Thysanoëssa and allied forms live close to the bottom by day (Otterström, 1910, p. 10 ; Lebour, 1924, p. 404 ; Hickling, 1925, p. 741 ; Russell, 1927, p. 588 ; Southern and Gardiner, 1932, p. 155 and Macdonald, 1927, p. 756).

On the other hand, there is also no lack of evidence that Euphausiids may occasionally be found right at the surface in broad daylight (Hickling, *loc. cit.*, p. 742 ; Bigelow, 1926, p. 145 ; Macdonald, *loc. cit.*, p. 776).

In the present experiment a note was made in the Log : " At 12.30 p.m. *Shrimp* were visible in the water." On this occasion (Station N. 234, 11.5.32) Euphausiids were seen in fair abundance, and a single specimen taken in a bucket of surface water was found to be *Th. inermis*. Herring larvæ and Eel (Anguilla) were present, but in smaller numbers. By 4 p.m. (Station N. 235) the Log records that the plankton was no longer to be seen. In the tow-netting made when *Shrimp* were known to be in the surface water only 20 specimens occurred, 13 *Th. raschii* and 7 *Th. inermis*.

The possibility that Euphausiids may avoid a net has been recognised by most observers (e.g. Holt and Tattersall, 1905, p. 137; Ruud, 1932, p. 14; Frost, 1932, p. 203, etc.), and although I would hold this responsible for a small part of the paucity of Euphausiids at Station N. 234, to ascribe to this cause the whole of the enormous discrepancies between day and night collections would surely be to endow these animals with powers of swimming altogether too great. Moreover, such an hypothesis would entail the bulk of the population remaining by day in the upper illuminated levels, where, in point of fact, Hickling (*loc. cit.*, p. 739) shows that they are almost certainly not to be found.

SAGITTA.

Whatever explanation we may accept for this phenomenon with regard to the Euphausiids, it is impossible to believe that in the case of Sagitta it is due to the animals avoiding the net. They are by no means active creatures and, moreover, are known on occasions to migrate downwards by day (Russell, 1931 and 1933). It is thus tolerably certain that the discrepancies between day and night catches are due to a proportion of the population moving downwards to levels below those fished by the net.

It is well established that Sagittas of different size do not respond in the same way to changes in light intensity, and the present material was examined to see whether there was any indication that one size group more than another had sunk to those levels which the net could not sample. In all, over two thousand specimens of *S. elegans* were measured and the mean length in each of the twenty collections determined. This was found to vary between 22 and 25 mm., but no correlation with the hour at which the sample was taken could be detected.

CALANUS FINMARCHICUS AND *CALANUS HYPERBOREUS.*

The differences between the daylight and dark collections, whilst significant, were not so marked in the case of these two species as in those considered above.

The large mesh employed with the ring-trawl retains no more than a small proportion of *C. finmarchicus* in Stage IV and on this account only specimens in Stages V and VI were enumerated. In the case of the larger *C. hyperboreus*, individuals in Stage IV were more abundant and were included in the counts.

It is known that the older and larger individuals tend to live below the younger (see Gardiner, 1933, p. 464; Marshall, 1933, p. 128) and thus might be expected to disappear from the daylight catches to a greater extent than the younger stages. In order to test this, the percentage of adult specimens (♂ and ♀) of *C. finmarchicus* occurring in the 20 collections, together with the mean figure for each of the periods of daylight and darkness was determined. These are set out in Table II. It will be seen that during the daylight, adults disappear from the population to a small, but definite extent. According to the test provided by Fisher (1930, p. 114) the difference between the mean percentages in darkness and daylight is a significant one.

TABLE II.

Percentage of Adult Specimens of C. finmarchicus Occurring in each of the Twenty Collections.

	Station.	Time.	Percentage of Adults (Stage VI).		Station.	Time.	Percentage of Adults (Stage VI).
Darkness.	N. 217	2024	62%	Darkness.	N. 227	2010	54%
	218	2206	77		228	2214	65
	219	0004	77		229	0008	64
	220	0151	57		230	0144	48
	221	0347	59		231	0342	43
			Mean 66%				Mean 55%
Daylight.	222	0628	51%	Daylight.	232	0623	35%
	223	0916	54		233	0855	57
	224	1214	54		234	1148	54
	225	1531	46		235	1529	38
	226	1819	37		236	1809	49
			Mean 48%				Mean 47%

SUMMARY AND CONCLUSIONS.

1. Twenty oblique hauls of a stramin ring-trawl, diameter of mouth 5 feet, were made during a period of 48 hours off Liverpool, Nova Scotia, in May, 1932.

2. The common species were *Thysanoëssa raschii*, *Th. inermis*, *Sagitta elegans*, *Calanus finmarchicus* and *C. hyperboreus.*

3. All of the above occurred in the collections made during the night in larger numbers than in those in the daytime. No such discrepancy appeared in the case of the Fish Ova.

4. The discrepancy is held to be due in each case to a proportion of the population sinking to depths greater than could be sampled by the net.

5. Adult *Calanus finmarchicus* tended to disappear to a relatively

greater extent than individuals in Stage V. No such phenomenon could be detected in the larger specimens of *Sagitta elegans*.

6. Discrepancies of this kind would have to be taken into account when lines of Stations are worked by day and night. The probability of error will be greatest where the mesh employed is large, and particularly so in those cases where the lowest levels are left unsampled.

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The Vertical Distribution of Marine Macroplankton. XII. Some Observations on the Vertical Distribution of *Calanus finmarchicus* in Relation to Light Intensity.

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With 3 Figures in the Text.

In my previous reports on the vertical distribution of plankton animals off Plymouth the apparent importance of light-intensity as a major factor in determining the behaviour of some species has been repeatedly stressed. The results appeared to show that individuals of a species, when in a state in which they react towards light, will congregate in those water layers in which certain optimum light conditions are to be found. There seems now to be no doubt that at certain times in the life-history of a plankton animal the strength of light has a predominating influence so that in a study of the habits of plankton animals the light conditions must be measured as being a factor of the environment of equal importance to such factors as temperature and salinity. Now that the observation of the light conditions has been made possible through the researches of Poole and Atkins we are in a position to study this factor in research on the ecology of plankton animals.

The first contribution to this line of research has been made by Clarke (2) on the basis of observations made in the Gulf of Maine in July and August, 1931. During the same period in that year in collaboration with Dr. Atkins I made a number of observations on the vertical distribution of plankton animals off Plymouth with simultaneous measurements of light intensity beneath the sea surface. It is with some of the results of this work that the present report is concerned.

As a working hypothesis it had been assumed that for some species there is an absolute light intensity optimum, but that while this optimum may remain constant for short periods of time it changes from time to time in accordance with the various changes in development during the life-history of the animal and may be different for different broods.

For a preliminary test of this theory it was felt that it was better to make a number of observations on different days than to follow an actual migration through 24 hours. If in the middle of the day on different days the animals were found to be living at depths at which they experienced similar light intensities, better proof of the theory would be obtained than by attempting to correlate the light intensity with the distribution of the animal during active migration, when such factors as the swimming speed of the animal and its speed of reaction might tend to prevent it from keeping accurately within the zone of optimum light conditions. During full daylight the animals would have had more time to congregate around the region of their true optimum.

Ideally the observations should be made either on cloudless days or on days of uniform dullness ; under such conditions the animals would show best the light conditions they prefer. On days of constantly changing illumination it is doubtful whether at any one time the animals will be found accurately concentrated round the actual optimum light conditions. Unfortunately some of the days on which my observations were made were anything but ideal in this respect.

Seven series of observations were made on five days, July 21st, 22nd, and 29th, and August 5th and 12th, 1931, two observations being made on the first and last of these days respectively. The collections were made with usually six nets fished simultaneously in a horizontal direction for half an hour. Light measurements were made by Dr. Atkins at different depths immediately before or after the collecting period, and the air illuminations were observed during the time the nets were fishing. Most of the collections were made at a position 2 miles east of the Eddystone Lighthouse, the depth being about 50 metres.

Collecting Methods.

In my previous researches I had fished only with one net, a series of catches being made consecutively at different depths. Under such conditions the period of time between the first and last hauls of a series of six collections must necessarily be considerable. If accurate comparison was to be made with light conditions it was therefore essential that the six nets should be fished simultaneously. It was necessary that the depth at which each net was fishing should be known, and as closing mechanisms were not used it was essential that the nets could be attached to and detached from the towing wire as quickly as possible.

The nets used were coarse silk nets of the international pattern (silk No. 3 ; 58 strands to the inch ; diameter of opening 50 cm.). The silk was however attached directly by a calico band to the ring without the half-inch meshing used in the international design (**8**, p. 7) : the ring was made of brass $\frac{3}{8}$-inch diameter (weight *ca.* 2 lb. $1\frac{1}{2}$ oz.).

If six nets be attached at intervals to a wire with a single weight at its end the wire will be considerably curved when the nets are fishing somewhat after the style of A in Figure 1, and it would be difficult to estimate the depth of any one net. For any fishing method it would certainly be extremely complicated, if indeed possible, to predict by calculation the actual depths at which the nets would fish. A practical attempt was made to overcome this difficulty by using the Admiralty depth-recorder as the end weight and by attaching a metre below each net a lead weight whose weight in water was the same as that of the depth-recorder in water (Fig. 1, B).

The accuracy of this method was tested by taking a successive series of hauls and interchanging the depth-recorder with each of the lead weights in turn. It was found that on this occasion the average depths of each of five nets were as follows :—

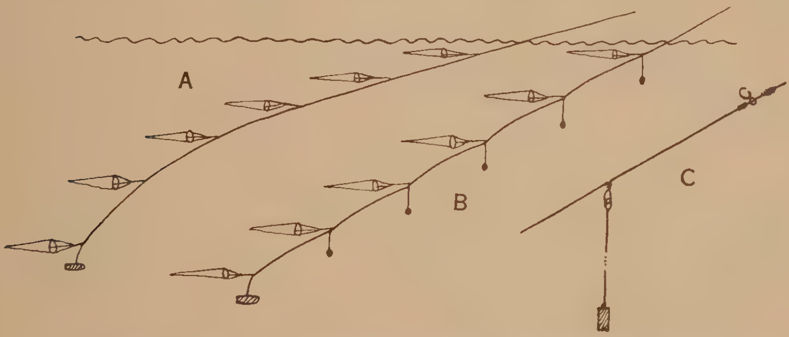

Fig. 1.—Fishing methods. A, with single weight at end of towing-wire ; B, with weights by each net on towing-wire ; C, method of attachment for nets and weights.

Surface, 7 m., 14·4 m., 22·6 m., and 29·5 m. : the depth intervals between each net were thus 7, 7·4, 8·2, and 6·9 m. These results were sufficiently close to enable one to assume that the nets in the other series of observations fished at approximately equal intervals of depth. In order to ensure that each series was hauled in exactly the same way and at the same speed a declinometer was hung on the wire as described in **8**, page 9. The angle aimed at was 30°, and by varying the speed of the ship's engine the pendulum was kept oscillating slowly about this angle. By observation of objects drifting past the ship's side it was found that with an average angle of 28·6° the speed averaged 1·2 knots : at an average angle of 31·2° it was 1·03 knots, and at 25·4° it was 1·42 knots : the extreme variation was thus probably between 1 and 1·5 knots.

In order to ensure rapidity of work the gear was attached in the following manner. The nets were fixed to the wire ($\frac{3}{4}$-inch circumference flexible steel) by signal halyard swivel clips: one half of each swivel was attached to a rope from the tow-net bridles; and the other halves were threaded on to the towing wire and fixed at intervals of 15 metres by stoppings of twine rove through the wire (Fig. 1, C). One metre below each swivel a small bight was made in the wire for the attachment of the lead weights. Each lead weight (*ca.* 9¼ lb. in air) had a length of rope with a slip-hook at its end. When shooting, a net was held by one man and a lead by another; as each bight and swivel attachment passed over the ship's side the net and weight were quickly hitched on without stopping the wire from coming off the winch; similarly each net and lead could be quickly detached as the wire came in. The errors due to the nets fishing in layers above their correct depths were thus reduced to a minimum. Each net was numbered serially to avoid confusion on deck; when all the nets were on board after fishing the washing down of the silk and preservation of the catches could thus be proceeded with carefully and at leisure.

The Light Conditions.

The details of the light measurements have already been published by Atkins and Poole (**1**, p. 141). Measurements were obtained with a gas-filled potassium cell under a diffusing filter. This cell was sensitive only to the blue end of the spectrum with a maximum sensitivity probably near a wave-length of 440 mμ. Observations were made immediately before or after the net collections so that figures could be obtained for the coefficients of absorption of the water at different depths. During the hauls a photometer was used on the roof of the ship's deck-house to measure the air illumination; a number of measurements were made while the nets were fishing and a mean value was taken. From these mean values and the knowledge of the coefficients of absorption of the water the submarine illumination was calculated for the depths at which the nets were fishing. The details of these illuminations are given in Table I.

On July 21st, 1931, immediately after the first series of collections, further measurements were made on the penetration of other wave-lengths of light, using a thin film caesium on silver vacuum cell, with red, yellow, green, and blue filters under opal. On August 12th measurements were also made of the penetration of the near ultra-violet light with a Burt sodium vacuum cell and a 10 mm. Corex red-purple filter.

Full details of the general weather and lighting conditions on the days on which collections were made are given in the log at the end of this report. At the same time records were obtained of the illumination for some hours prior to the times of collecting by the photo-electric continuous light recorder on the roof of the Plymouth Laboratory. Although these results will not be a faithful reproduction of the light conditions ten miles out to sea where the collections were made, they nevertheless serve as a good guide to the average illuminations obtaining when our observations were made. The results are reproduced in Figure 2. It can be seen that on no day were the light conditions ideally constant; on the other hand at the times that collections were made the light was evidently not varying as badly as it might have done. Examination of Figure 2 shows that on July 21st at the times when Series I and II were made the light conditions had become tolerably constant which is in agreement with the observations made on the ship and given in the log. On July 22nd the conditions had been fairly constant, increasing steadily until a short time before the period of collecting when they became more varied. On July 29th for an hour before the collections were made the illumination had been increasing and decreasing on a very smooth curve, but became more varied at the time of collecting. On August 5th both prior to and during the time of collecting there were a few short periods of increased intensity but on the whole the light had been varying constantly within small limits. On August 12th conditions had been varying to about the same extent as on August 5th but had been consistently low.

Of the five days July 21st was the only bright day; the other four days, and particularly the last three were dull and overcast.

Examination of Figure 2, page 145 in the paper by Atkins and Poole (**1**) shows that for the five days (Series 55, 60, 61, 67 and 75 *loc. cit.*) the transparency of the water had been much the same, and that the transparency varied very little at different depths except on August 12th (Series 75) when the water became appreciably clearer in the deeper layers. Also "in Series 61 (July 29th) the zone of less transparent water, $\mu =$ 0·173 is found at 5–10 m., instead of 0–5 m." (**1**, p. 148). From these results I have calculated the depths at which the following intensities would, at the time of collecting, have been found on each day, viz. 80, 60, 40, 20, 10, 5, 4, 3, 2, 1, and 0·5 thousands of metre-candles. These have been plotted on Figure 3, drawing the curves of equal illuminations for the seven series of observations.

As a result of further photo-electric measurements on July 21st and August 12th we can get an approximate picture also of the penetration of light of different wave-lengths beneath the sea surface. Examination of Figure 5, p. 153 in **1**, shows that for the wave-lengths 580 mμ to 440 mμ, yellow→green→blue, there is comparatively little difference in the amount of absorption at any rate down to 30 metres. But light at the red end of the spectrum 660 mμ to 760 mμ is much more rapidly absorbed and has become reduced to 1 per cent of the illumination immediately below the surface before a depth of 10 metres has been reached. The violet and near ultra-violet rays, to 360 mμ, however, penetrate slightly further than

TABLE I.

Vertical Illuminations, V, in Thousands of Metre Candles, at the Depths (*d*), in Metres, at which the Six Nets were Fishing.

The depth of the water was about 50 m., and position 2 miles East of Eddystone Lighthouse. *r*=illumination on deckhouse roof.

Date 1931, July	21st.		21st.		22nd.		29th.		Aug. 5th.		12th.		12th.	
G.M.T.	2.24–2.54 p.m.		5.54–6.24 p.m.		11.11 11.41 a.m.		11.39 a.m.-12.9 p.m.		11.19–11.39 a.m.		10.55–11.25 a.m.		3.7–3.32 p.m.	
Series	I		II*		III		IV		V		VI		VII*	
	d	V	*d*	V	*d*	V	*d*	V	*d*	V	*d*	V	*d*	V
In air	*r*	88·6	*r*	27·1	*r*	91·5	*r*	50·0	*r*	26·9	*r*	35·4	*r*	45·8
1.	0·5	80·8	0·5	24·7	0·5	72·8	0·5	45·4	0·5	22·0	0·5	24·4	0·5	31·6
2.	7·2	34·4	7·9	9·36	8·1	19·7	7·1	16·4	7·2	7·05	7·5	11·5	7·0	15·7
3.	14·3	13·2	15·7	3·32	16·1	6·63	14·4	6·55	14·3	2·42	14·9	4·34	13·8	6·65
4.	21·4	5·18	23·5	1·24	24·1	2·78	21·7	2·22	21·4	0·88	22·3	2·07	20·6	3·11
5.	28·5	2·39	31·3	0·54	32·1	1·39	29·0	1·29	28·5	0·47	29·7	1·08	27·4	1·66
6.	35·6	1·03	39·1	0·16	40·1	0·43	36·3	0·53	–	–	37·1	0·58	34·2	0·91

* Had drifted a little further in.

do the red rays and are not reduced to 1 per cent until after 15 metres have been reached.

It is interesting that as regards the shorter anti-rachitic ultra-violet rays Atkins and Poole write, " Hulbert's coefficients have been used to show that even in the clearest ocean waters the anti-rachitic portion of the spectrum is reduced to 1 per cent of its subsurface value at 1·1 to 2·2 m., according to wave-length, and to 0·001 per cent at from 2·9 to

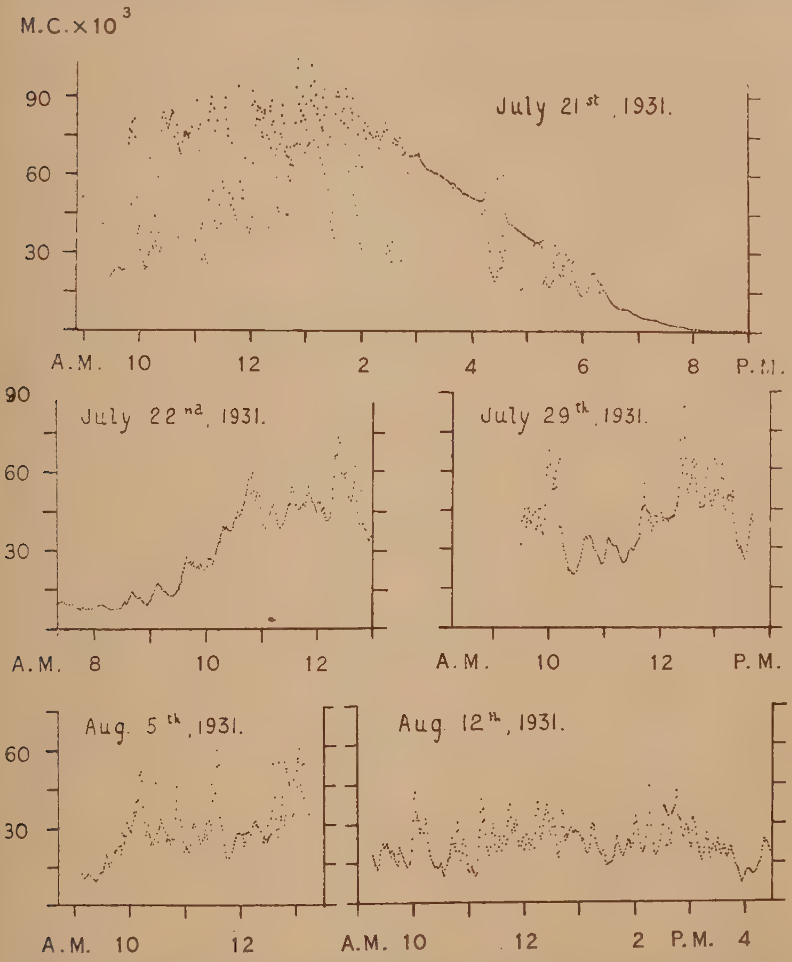

Fig. 2.—Records of light intensity obtained on roof of Plymouth Laboratory with vacuum photo-electric cell and thread-recorder, on July 21st, 22nd, and 29th, and August 5th and 12th, 1931. (By courtesy of Dr. W. R. G. Atkins.)

5·5 m." They suggest, however, that "it also seems possible that, though anti-rachitic action is but feeble at wave-lengths longer than 313 $m\mu$, yet owing to their better penetration those somewhat longer than the limit given may be more effective in sea-water."

THE VERTICAL DISTRIBUTION OF *Calanus finmarchicus* IN RELATION TO LIGHT CONDITIONS.

In working up the material of the collections all the species were counted. It has, however, been shown previously that in order to elucidate the principles underlying the behaviour of the animals it is useless to work on a mixed population; the population of any one species needs to be further analysed into the sexes and stages of development occurring therein. This further analysis has only been done for the copepod, *Calanus finmarchicus*, and in this paper I deal only with adult males and females. Owing also to the possibility of differences in behaviour shown between different broods it is necessary to make a further analysis of the Calanus by making size measurements as these may indicate differences in the populations occurring from day to day.

The general results of these observations on adult Calanus are given in Figure 3, which shows the percentage vertical distribution of the females and males on the days in question. The actual numbers of Calanus in the catches are given in Table II on page 583; it can be seen that the numbers are fully large enough to be significant. On the diagram in Figure 3 are also given the lines of equal illumination in thousands of metre-candles calculated as explained previously (see page 573). Underneath the depth distribution diagrams for each sex are given the median lengths (Q_2) and upper and lower quartiles (Q_3 and Q_1) being the lengths between which 50 per cent of the population lay on each day. The length measurements are the total length of the body to the end of the caudal furca but excluding the furcal setæ. A number of both sexes were measured from every catch (Tables III and IV, pp. 583 and 584). In estimating the median length the numbers measured at each depth in a series were added together. Gardiner has shown that there may be a slight difference in the depth distribution between individuals of different sizes in Stage V, the larger individuals in a population being deeper (**3**, p. 590); see also Marshall (**4**, p. 123). Insufficient numbers were measured on this occasion to show significant differences in size-composition of the catches from different depths, but it was evident that such difference if it occurred would not have been of the order of the differences that will be referred to later between one whole population and another in July and August.

An examination of Figure 3 shows that during the four observations in July (Series I–IV) the majority of the female Calanus were near the surface and living in the very high light intensities of 20,000 metre-candles and more: below 10,000 metre-candles the remaining Calanus appear to be evenly distributed. In August (Series V to VII) there is a definite change in the vertical distribution, the female Calanus now avoiding light intensities of 20,000 metre-candles and over. This change is very noticeable and at first sight would have been regarded as a change in the behaviour of the animal. A study of the length measurements shows, however, that instead of there being a change in behaviour there has been a change in population. We are quite definitely dealing with a different population in August from that we had in July. In July the median lengths of the female Calanus in the Series I to IV were 3·186, 3·169, 3·170, and 3·141 mm. respectively, while in August for Series V to VII these lengths were 3·068, 3·000, and 3·013 mm. The change in population receives further confirmation from the appearance in August catches of numbers of early stages of Calanus, whereas in July the catches consisted almost purely of adults. In August we have possibly therefore a new brood of adults which have just grown up, or one consisting perhaps of the smaller individuals that may be produced towards the end of a breeding period (Marshall, **4**, p. 122).* This difference in behaviour between different populations is in keeping with previous observations (**7**, p. 438) which led to the suggestion that the different broods were physiologically distinct and showed differences in their behaviour towards light intensity. It emphasises at once the danger of attempting to make conclusions on the effects of the environment on an animal without a certain knowledge of the population under examination. Analysis of the vertical distribution results of the female Calanus on July 29th and August 5th, 1931, would certainly have led to wrong conclusions if length measurements had not been made at the same time. If we turn now to the results for the male Calanus we notice a similar change in depth distribution coincident with a change of population. The male Calanus were living deeper in the water than the females and tended very definitely to avoid those high light intensities in which the females were living. In July (Series I to IV) the male Calanus definitely avoided intensities of 40,000 metre-candles and over, but below about 20,000 metre-candles they were rather evenly distributed in the water though there are indications in Series II and IV that they tried to keep above intensities of 500 metre-candles and less. In August (Series V to VII) the majority of the males were deeper in the water than in July and were now avoiding intensities as low as 10,000 metre-candles. Here again we find length differences between individuals

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* A number of female Calanus were stained and examined for state of maturity. In the limited number examined no significant difference could be found in the proportions of the different degrees of maturity occurring in the July and August populations. I am very grateful to Miss S. M. Marshall and Dr. A. G. Nicholls for examining these specimens for me.

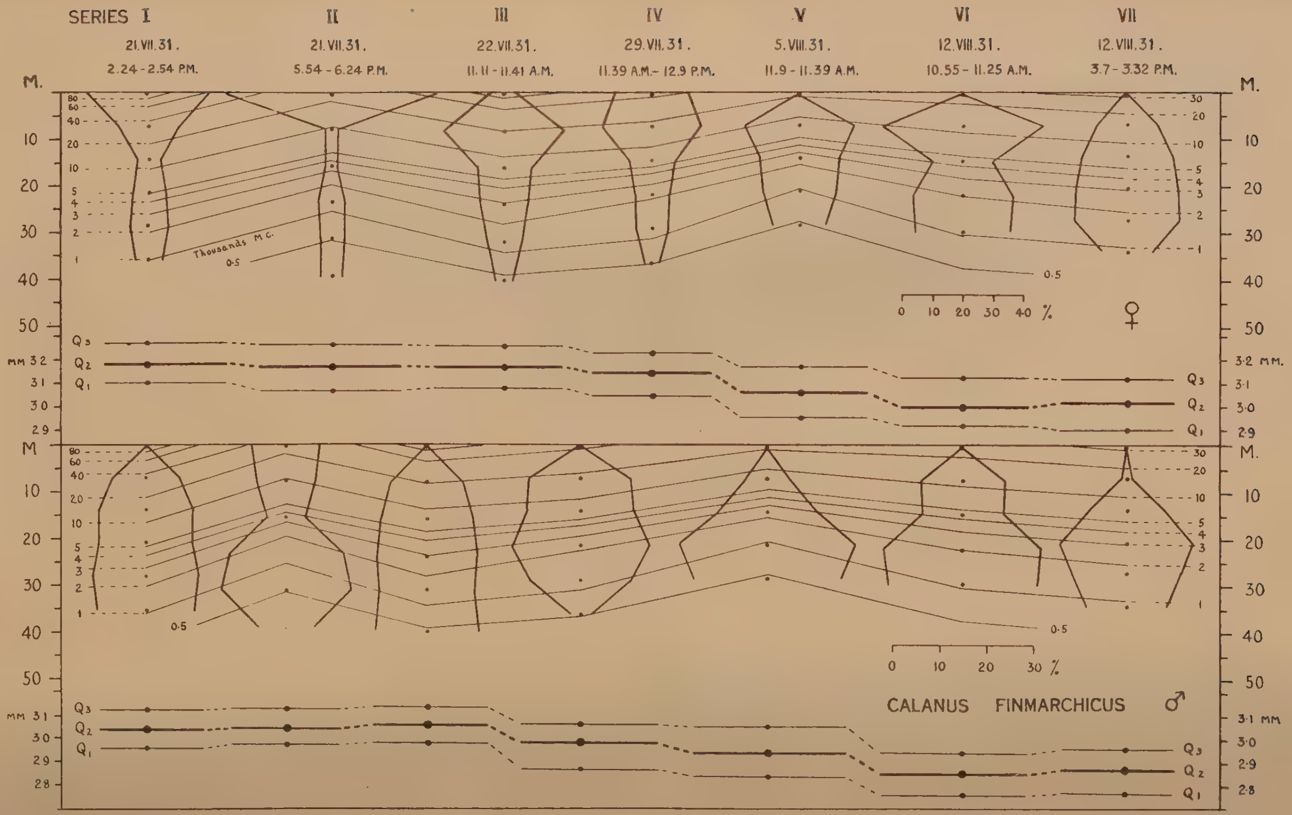

Fig. 3.—Percentage vertical distribution of adult *Calanus finmarchicus*; females above, males below. The black spots indicate the depths at which the nets were fishing. For each day are plotted the light intensities beneath the surface and these points are joined to form the isointensity lines of 80, 60, 40, 20, 10, 5, 4, 3, 2, 1, and 0·5 thousands of metre-candles. Below each diagram is given the medium length (Q_2) and upper and lower quartiles (Q_3 and Q_1) of the Calanus. (The diagrams for the males Series II, III, and IV are slightly to the left of those for the females.)

of the July and August populations. While in Series I to III in July the median lengths were 3·034, 3·043, and 3·060 mm., in August, Series VI and VII, they were 2·837 and 2·873 mm. In Series IV and V, however, at the end of July and beginning of August they occupied an intermediate position of 2·987 and 2·943 mm. respectively, which may have indicated a mixing of the two populations.

This tendency for the males to avoid the bright intensities that the females can endure is in keeping with previous results for this region (**7**, p. 442). The very even distribution assumed below the upper limit at times appears also to be somewhat characteristic of the males and seems to imply a less sharply graded sensitivity to light intensities between the upper and lower limits than is shown by the females. This type of distribution for the males has recently been shown also by Nicholls (**5**, p. 146) to occur in the Clyde Sea area, where at different times during the day this difference in behaviour between male and female is clearly indicated. It is interesting that in the observations made by Nicholls the upper limit of intensity avoided by the male Calanus would appear to be as high as that avoided by females on the same day.

On the whole the present results appear to support the light optimum theory referred to above (p. 569). The preference of the July individuals for higher intensities than the August individuals is consistent. Very close agreement is shown between the distribution of the females and the light conditions in the two Series of observations made on July 21st (Series I and II). Between 2.24 and 2.54 p.m. the threshold intensity for stimulation of upward movement seems to have been somewhere between 20,000 and 10,000 m.c. By 5.54 to 6.24 p.m. the female Calanus have crowded very much more towards the surface and the threshold illumination still appears to lie at about 20,000 m.c. The males also show agreement in that while at 2.24 to 2.54 p.m. the upper limiting intensity was about 60,000 m.c., at 5.54 to 6.24 p.m., when intensities of 40,000 m.c. and over could no longer be experienced, the male Calanus had extended their distribution to the surface.

It is difficult, however, from these observations to decide on the optimum conditions except within very wide limits. The female Calanus, for instance, in Series III and IV would appear to have a slightly lower optimum than those in Series I and II. It is interesting, however, that if these four observations be arranged in the order of the time of day at which they were taken the Calanus are found to have slightly increasing optima, which might point to increasing adaptation on the part of the Calanus throughout the day. No such increase is, however, shown in the two series taken on August 12th (Series VI and VII). We must wait for further observations to be made before we can decide the cause of these discrepancies or whether indeed they may not be false impressions brought about by the inability of the animals to keep accurately to their optima during rapid fluctuations in light intensity.

These collections were made at a time of year when Calanus is living nearer the surface than earlier in the year. The present observations confirm the results of two previous years (**6** and **7**), although the August population was living deeper than might have been expected. It is possible, however, that they are more recently moulted from Stage V than those occurring in the July collections and have not yet developed to the age at which they desire bright light. It should also be mentioned that the upper water layers were considerably warmer on August 12th than on July 22nd, the temperatures at 15 m. being 15·0°C. and 12·4°C., respectively (see Log, p. 582).

It is a great pleasure for me to thank Dr. W. R. G. Atkins for his willing co-operation and assistance in this work, and for his kind permission to reproduce the light measurements in Figure 2. My thanks are also due to Captain Lord and the Crew of s.s. *Salpa* for their great help while the collections were being made, and to my wife for the assistance she gave me in helping to sort and count the collections.

SUMMARY.

1. Observations are given on the vertical distribution of adult *Calanus finmarchicus* in the daytime off Plymouth in July and August, 1931, as a result of collections made simultaneously with the photo-electric measurement of submarine illumination.

2. A series of nets, usually six, was towed simultaneously in such a manner that the depth of each net was known approximately.

3. The female Calanus in July preferred higher intensities of light than did the females in August; this change was coincident with a change in the Calanus population as shown by size measurements. A similar change in distribution and in population was shown by the males.

4. The females in July were living in intensities of 20,000 m.c. and more; but those in August were avoiding such high intensities. The males in July avoided intensities of 40,000 m.c. and over, while in August their upper limit was about 10,000 m.c.

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Log.

July 21*st*, 1931.

From 12.15 p.m. until 1.25 p.m. there had been high clouds and blue sky, but the sun was partially obscured : from then until 1.55 p.m. the sun shone brightly in a clear sky, with cumulus coming up on S.W. horizon, and wind freshening slightly from the west. At 1.55 p.m. a very thin sheet of high cloud passed over the sun but barely obscured it. The sea surface was calm, with slight swell and lop.

Series I. 2 miles East of Eddystone.

Six nets fished together on 75 metres of wire : nets 15 metres apart. Depth recorder and 5 weights (*ca.* $9\frac{1}{4}$ lb. in air) each one metre below nets. Nets= coarse silk international without front meshing.

The sky was quite cloudless for the whole haul, almost over the whole sky except the horizon.

2.24–2.54 p.m.

Average depths of nets. Surface, 7·2, 14·3, 21·4, 28·5, and 35·6 m. Nets took 4 min. 35 secs. shooting ; and 4 min. 6 secs. hauling.

3.45 p.m. Cloudless sky. 5.23 p.m. Almost cloudless sky except for a little wispy cirrus. 5.38 p.m. Sun going behind a cloud.

SERIES II. By this time we had drifted to near L4, half-way between Breakwater and Eddystone.

5.54 p.m.–6.24 p.m.

Six nets as in Series I, fishing at average depths of surface, 7·9, 15·7, 23·5, 31·3, and 39·1 m.

At 5.58 the sun came out clear again.

Nets took 3 min. 35 secs. shooting; and 2 min. 38 secs. hauling.

Sun was shining all the time after 5.58 p.m.

July 22nd, 1931.

8 a.m. Very dull and patches of fog. 10.45 a.m. Clearing and sun shining enough to throw shadows. Had been dull up to now. 11 a.m. Sun shining fairly fully through thin sheet of low cloud.

SERIES III. 2 miles East of Eddystone: sea choppy. Six nets fished as in previous series.

11.11 a.m.–11.41 a.m.

Nets fished at average depths of surface, 8·1, 16·1, 24·1, 32·1, and 40·1 m.

Nets took 2 min. 37 secs. shooting; and 1 min. 59 secs. hauling.

1 p.m. Secchi disc 9 m. on windward side: 8 m. on leeward side. Temperatures of sea: surface, 14·5° C.; 5 m., 13° C.; 10 m., 12·8° C.; 15 m., 12·4° C.; 25 m., 12·2° C.

July 29th, 1931.

S.W. wind: slight lop. It had been dull with the sun covered all morning. Cloud-sheet was of uneven thickness, so that the light was variable.

SERIES IV. 2 miles East of Eddystone.

Six nets fished as previously.

11.39 a.m.–12.9 p.m.

Nets fished at average depths of surface, 7·1, 14·4, 21·7, 29·0, and 36·3 m.

Nets took 2 min. 23 secs. shooting and 2 min. 18 secs. hauling.

Secchi disc: 7 m. on weather side; 8 m. on leeward side. The sun was covered the whole time but the cloud-sheet was of very uneven thickness.

August 5th, 1931.

It had been dull with thick low clouds all morning; at 9.55 the sun was trying to show through a slight break in the clouds. Calm. S.E. breeze.

In shooting lost one net so started again with five.

SERIES V. 2 miles East of Eddystone.

11.19–11.39 a.m.

Nets fished at average depths of surface, 7·1, 14·4, 21·7, and 29 m. Nets took 2 min. 5 secs shooting; and 1 min. 46 secs. hauling.

Secchi disc: 10 m. on weather side; 12 m. on leeward side.

August 12th, 1931.

Sea calm at first; clouds all over sky; low nimbo-cumulus type at about 1500 ft.

SERIES VI. 2 miles East of Eddystone.

10.55 a.m.–11.25 a.m.

Nets fished at average depths of surface, 7·5, 14·9, 22·3, 29·7, and 37·1 m. Bottom net touched bottom while shooting. Nets took 3 min. 8 secs. shooting; and 2 min. 50 secs. hauling.

Secchi disc: 12½ m. on weather side; 15 m. on leeward side.

1·45 p.m. Temperatures of sea. Surface 15·1° C.; 5 m., 15·1° C.; 10 m., 15·04° C.; 15 m., 15·0° C.; 20 m., 13·7° C.; 30 m., 13·4° C.

2.30 p.m. Sun shining through clouds.

SERIES VII. 2 miles East of Eddystone.

3.7–3.32 p.m.

Nets fished at average depths of surface, 7·0, 13·8, 20·6, 27·4, and 34·2 m. Nets took 2 min. 49 secs. shooting; and 2 min. 30 secs. hauling.

3.25 p.m. Secchi disc 15 m. on leeward side.

Haul ended about 4 miles E.N.E. of Eddystone.

TABLE II.

NUMBERS OF CALANUS FEMALES AND MALES IN EACH CATCH.

D, average depth of each haul. S, surface.

	Series I.			Series II.			Series III.	
	July 21st, 1931.			July 21st, 1931.			July 22nd, 1931.	
D.	♀	♂	D.	♀	♂	D.	♀	♂
S.	22,726	186	*S.*	70,000	6,088	*S*	980	–
7·2	11,669	5,321	*7·9*	4,880	5,108	*8·1*	4,233	2,568
14·3	4,822	7,360	*15·7*	4,315	3,377	*16·1*	1,952	3,355
21·4	6,384	7,310	*23·5*	9,555	10,221	*24·1*	1,674	3,648
28·5	7,420	8,283	*31·3*	8,986	11,520	*32·1*	1,373	3,432
35·6	5,038	7,563	*39·1*	8,076	4,814	*40·1*	690	3,698

	Series IV.			Series V.			Series VI.			Series VII.	
	July 29th, 1931.			Aug. 5th, 1931.			Aug. 12th, 1931.			Aug. 12th, 1931.	
D.	♀	♂	D.	♀	♂	D.	♀	♂	D.	♀	♂
S.	5,010	53	*S.*	7	–	*S.*	26	1	*S.*	127	3
7·1	6,592	1,071	*7·1*	1,215	100	*7·5*	8,664	1,655	*7*	2,179	204
14·4	3,290	1,128	*14·3*	854	214	*14·9*	3,300	1,620	*13·8*	3,270	1,357
21·7	2,401	1,449	*21·4*	801	378	*22·3*	5,478	3,087	*20·6*	3,697	2,418
29·0	2,164	1,047	*28·5*	579	322	*29·7*	5,170	2,902	*27·4*	3,834	1,952
36·3	1,118	221							*34·2*	1,825	1,460

TABLE III.

LENGTHS OF CALANUS IN MILLIMETRES AS MEDIAN (Q_2), AND UPPER (Q_3) AND LOWER (Q_1) QUARTILES.

		Females.			Males.		
		Q_1	Q_2	Q_3	Q_1	Q_2	Q_3
July 21st.	Ser. I	3·102	3·186	3·275	2·955	3·034	3·119
„ 21st.	„ II	3·068	3·169	3·266	2·973	3·043	3·125
„ 22nd.	„ III	3·079	3·170	3·259	2·984	3·060	3·136
„ 29th.	„ IV	3·045	3·141	3·227	2·875	2·987	3·066
Aug. 5th.	„ V	2·958	3·068	3·171	2·840	2·943	3·055
„ 12th.	„ VI	2·921	3·000	3·127	2·768	2·837	2·943
„ 12th.	„ VII	2·899	3·013	3·117	2·776	2·873	2·965

TABLE IV.

MEASUREMENTS OF TOTAL LENGTHS OF CALANUS IN MILLIMETRES.

	FEMALES.							MALES.						
	I.	II.	III.	IV.	V.	VI.	VII.	I.	II.	III.	IV.	V.	VI.	VII.
	July 21st.	" 21st.	" 22nd.	" 29th.	Aug. 5th.	" 12th.	" 12th.	July 21st.	" 21st.	" 22nd.	" 29th.	Aug. 5th.	" 12th.	" 12th.
MM.														
2·53	–	–	–	–	-	1	–	–	.	–	–	–	–	–
2·585	–	–	–	–		1	–	–	–	–	1	1	2	3
2·64	1	1	–	1	–	2	–	–	–	–	–	2	5	2
2·695	–	–	1	–	2	5	2	–	1	2	–	1	4	5
2·75	–	–	1	2	1	6	13	6	1	1	3	5	13	13
2·805	2	2	2	6	7	12	17	6	6	9	7	6	19	23
2·86	5	7	4	12	20	24	33	13	7	8	15	10	18	16
2·915	9	9	–	11	23	30	38	29	15	16	11	11	22	23
2·97	11	16	8	25	27	36	40	28	21	25	14	13	14	18
3·025	29	15	19	34	37	55	52	62	45	48	26	11	10	15
3·08	34	34	18	56	40	50	48	47	36	60	16	7	4	8
3·135	61	39	31	67	41	38	–	53	36	56	13	5	6	4
3·19	85	50	34	83	37	35	27	34	27	31	8	9	2	3
3·245	71	41	33	56	33	16	22	15	11	22	2	1	–	1
3·30	70	42	29	47	11	16	18	8	5	12	–	1	–	–
3·355	41	27	19	27	10	6	5	2	2	1	2	1	–	–
3·41	25	9	6	7	4	3	1	–	1	1	1	–	–	–
3·465	9	7	4	6	1	1	2	–	–	–	–	–	–	–
3·52	6	4	–	5	–	1	–	–	–	–	–	–	–	–
3·575	–	3	1	–	1	–	–	–	–	–	–	–	–	–
3·63	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Totals	461	306	210	445	295	338	366	303	214	292	119	84	119	134

Seasonal Changes in Biomass of *Calanus finmarchicus* in the Plymouth Area in 1930.

By

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With 8 Figures in the Text.

THIS paper deals with seasonal changes in the biomass of the copepod, *Calanus finmarchicus.* The work was carried out at the end of 1930 in the Laboratory of the Marine Biological Association at Plymouth with all the material of 1930 at my disposal.*

I take this opportunity of expressing my sincere thanks to the Director of the Plymouth Laboratory, Dr. E. J. Allen, for his ready assistance and for permission to work in the laboratory. I am much indebted, too, to E. Ford, V. A. Jaschnov, L. A. Zenkewitch for their valuable advice; particularly my heartiest thanks are due to F. S. Russell for supplying me with material and for the great assistance he has invariably given me throughout the present work.

"By biomass (Demoll) we term the quantity of substance in living organisms per unit of surface or volume. The biomass may be considered at some particular moment, the average yearly, seasonal, monthly, etc." (L. A. Zenkewitch, 1931.)

Weighing is the main method of obtaining the biomass. The conception "biomass" may be applicable also to the quantity of substance, characteristic for a given species at its different stages of development; it may even be applied to a single specimen. It is to be understood, then, that by biomass of a species or organism I mean here the quantity of substance in a living organism at a given moment. This quantity of substance is a characteristic of a given species just as are its size and morphological characters. The variations of biomass with seasons, locality, or in connection with age or different conditions of the medium, and the quantity of substance available for the species and the fluctuations of this quantity from stage to stage, form a definite complex, the study of which is a great problem.

* Interesting papers by Marshall and Nicholls have appeared recently in the Journal of the Marine Biological Association (Vol. XIX, No. 1, August, 1933) in which some of the questions discussed in the present paper are considered and confirmed.

The determination of the biomass of plankton organisms is of no small importance as a means for the quantitative investigation of the biomass of the plankton. At present quantitative investigations on the biomass of the plankton must be conducted so as to show the weight value of separate components in the total biomass of the plankton, or in the food ration of the plankton-feeding organism (consumption of plankton). The solution of this problem depends on a knowledge of the fluctuation of the biomass, since the plankton community is exceedingly changeable both in time and space. The same quantity of biomass may be formed of different components. One efficient method is to use the average weight, i.e. *the biomass of a given species of plankton organism*, as a coefficient for finding the weight, when the number of specimens is known. Thus we obtain the biomass of each component and of the whole plankton sample, and the relation of the given component to the total biomass. This relates equally to the food of plankton-consuming organisms. Thus plankton in any sea area or fresh-water basin and plankton as food are comparable—both sides of the investigation of the plankton biomass being solved by making use of the same coefficients (average value of the plankton organism's biomass).

Attempts to estimate the weight of plankton organisms were made long ago. Apstein (1896) gives a number of determinations for specimens of the fresh-water plankton ; Hensen (1887) records data on marine plankton ; Vernadsky and Vinogradov (1927) have emphasized the necessity of characterizing each species by average weight. But these attempts were not systematic ; moreover they have not been applied to investigations of the plankton biomass in order to elicit the role of the separate components. Therefore the investigation of the biomass of plankton lags behind similar investigations on the benthos and the feeding of the benthos-consuming organisms. It is impossible to apply the methods used in the study of benthos to plankton investigations for purely technical reasons. The examination of each plankton sample, or food supply, of a plankton-consuming organism, would take too much time ; the selected quantity of each species also does not guarantee the possibility of weighing it on account of its minute weight.

Therefore, without finally deciding on the method of estimating the average biomass of the species, whether it be selection of great quantities of a given species in the case of the larger forms, or the weighing of whole cultures of the smaller forms, especially in phytoplankton, or the estimation of the biomass of the organism on the basis of body-volume—I myself consider the method of estimating plankton biomass described above as fundamental if the question is to be attacked from the view-point of dynamics.

The apparent technical difficulties of obtaining the biomass of the plankton organism are in fact not so difficult to overcome. The advantage of such determinations—the biomass having been once found for the organisms of a given area—lies in the possibility of applying the obtained values to further investigations, connected with the estimation of the quantity of substance (biomass). Also old quantitative data on the plankton may be used. This calculation may be made at present in round figures, using the range of the quantity of the biomass of the plankton organism so that the different fluctuations in the biomass of any organism do not affect the total biomass of the whole plankton and its separate groups. It is, however, of considerable interest for further detailed estimations of the plankton biomass in that it raises various questions of the actual problem of " organism and medium."

MATERIAL.

The material was obtained by regular half-hour oblique hauls with the 2-metre stramin ring-trawl two miles east of the Eddystone Lighthouse during 1930. Since the hauls were made with a large-meshed net only the largest copepodite Stages IV, V, VI males and females of *Calanus finmarchicus* were caught ; Stage IV was barely represented.

The material upon which I worked was collected on the following dates : February : 12th, 19th, and 26th. March : 5th, 12th, and 27th. April : 11th, 16th, 24th. May : 7th, 15th, and 22nd. June : 10th, 19th, and 26th. July : 4th and 9th. August : 7th. September : 3rd and 16th. October : 1st, 14th, and 16th. November : 13th and 26th ; and December : 3rd, 10th, 17th, and 22nd.

METHODS.

I made the following determinations : raw weight ; dry weight ; and length of the body.

The weighing of live specimens presents a number of difficulties, and fixed specimens were used instead. Our material was fixed in formalin. The use of other fixatives may strongly affect the material (Vinogradov, 1927).

1. *Raw weight* was determined according to the quantity of material available in the following manner :

(*a*) When material was scarce (up to 300 specimens per sample) all copepodid stages in the sample were selected separately ; the selected quantity was then divided into 2–3 portions according to the number of specimens of a given stage, and each portion was weighed separately.

(*b*) When a given stage was numerous five portions were taken, each containing not less than 100 specimens of each stage.

The preparation of specimens for raw weighing is of paramount importance. To obtain the raw weight all the moisture must be taken off the body; this is no easy task. The usual method of drying in filter-paper (Bogorov, 1933) depends greatly on the individual capacities of the worker and on the conditions under which the weighing is performed; thus the results obtained are not always suitable for comparison, being no more than an index of the range of value of biomass. These deficiencies in the filter-paper method stimulated the working-out of more efficient methods, and I worked out such a method with the kind help of E. M. Kreps.

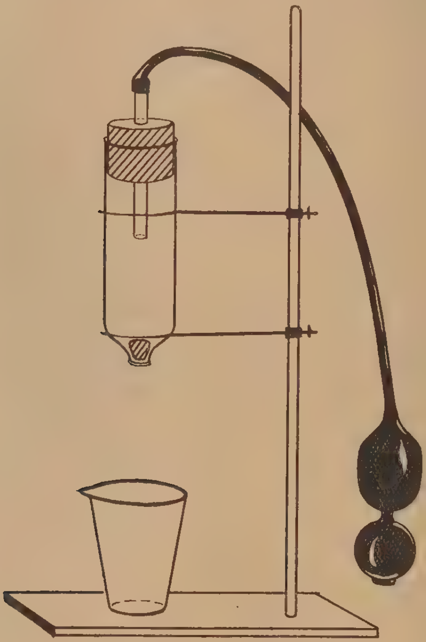

FIG. 1.—Device for "liquid" drying, to drive away water from the body-surface.

This method was based on the driving away of the moisture of the body surface by means of a dripping liquid. A device was constructed as follows: A small test-tube, not over 10 c.c., with a conical bottom and a hole in the apex of the cone, is fixed in a support. A glass ball, closing the lower aperture is placed at the bottom of the test-tube. The sides of the ball are somewhat flattened, forming facets, so as to let the liquid run freely out of the tube; but these facets must be of such a size that none of the specimens are washed out of the tube with the dripping liquid. This test-tube is stopped at the top by a cork, with a glass tube connected by rubber tubing with an air-pumping balloon (Fig. 1).

A weighed portion of the organisms was placed at the bottom of the tube; after all the water, brought with the portion, had been driven down the aperture of the tube, 1 c.c. of 90% alcohol was poured into the test-tube which, running down in a few seconds, brought away all the moisture of the body surface. Then 1 c.c. of ether was poured into the test-tube; the ether, running down rapidly, drove away the remaining alcohol. Then the test-tube was stopped, and air pumped through it for 30–60 seconds, according to the quantity of specimens, to drive out the ether vapour. The degree of dryness was decided arbitrarily, drying being continued until no apparent signs of liquid were left on the surface of the body. When immersed in water most of the specimens sank to the bottom. The exact degree of drying is somewhat indefinite, but after a short training some homegeneity is obtained. The use of measured quantities of fluid gives this method an appreciable advantage over the filter-paper drying method.

As is well known, alcohol extracts a good many substances (Vinogradov, 1927), over 10% in weight. In order to evaluate the method and to find the amount (in weight) of substances extracted by the rapid flow of alcohol and ether in our device, the resulting liquor was analysed. It was found to contain a negligible quantity of extracted substances, fluctuating from 1 2%. As compared to the filter-paper drying method the weight after " liquid " drying is somewhat smaller, but the range of fluctuation between separate weighings is clearly in favour of " liquid " drying.

2. *Dry weight.* The study of specimens by dry weight has many advantages over that by raw weight as it is evidently more accurate and supplies data of actual weight of the body-substance. The dry weight is thus a better characteristic of biomass and it should become the main unit in the determination of biomass.

The raw weight data depend chiefly on the quantity of water contained in the body, not on the quantity of substance of an organism, and the quantity of water in the body of different organisms is variable and depends on different conditions.

To find the dry weight a dessicator containing calcium chloride was used. After obtaining the raw weight the same organisms were placed on the grid of a dessicator on a weighed cover-slip. The material remained in the dessicator usually for two or three days, and weighing was repeated not less than three times at one-day intervals. If the last two weighings were equal the material was considered sufficiently dried and the counts were made.

The figures of dry weight thus obtained are not figures of *constant* dry weight. To obtain the latter the method must be considerably improved by drying in a high-temperature thermostat, or for a very long time. Yet this method gives figures, which, although not of absolute constant dry weight, are still constant to some degree, and fit for comparison, giving a much truer picture of the quantity of substance of an organism than does raw weight. The simplicity of operation, the little time needed, the portability and accessibility of the applied method and the comparative exactitude of the data obtained, tend to uphold dry weight as the best method for obtaining the biomass.

Both dry and raw weights were obtained on the Sartorius analytical balance.

3. The *length measurements* were made with a micrometer eyepiece. The total length was measured from the front edge of cephalothorax to the end of caudal furcæ, the furcal setæ being excluded.

RESULTS.

The results of weighing and measurement clearly show that both biomass and size of Calanus throughout the year are not constant but undergo changes, which so far as weight is concerned may be as great as twice their value.

The data show that the maximum of raw weight (Table I) was observed in May. Stage V (7th May), 0·7 mg. ; adult males (15th May), 1·13 mg. ; and females (15th and 22nd May), 1·10 mg.

The minimum weights were for Stage V, 0·35 mg. (14th October and 13th November) ; adult males, 0·50 mg. (13th November) and females, 0·41 mg. (16th October). The maximum range of fluctuation was for Stage V, 0·35–0·70 mg. ; for adult males, 0·50–1·10 mg. ; for females, 0·41–1·10 mg.

The maximum dry weight for all stages (see Table II) occurred on 15th May : Stage V, 0·252 mg. ; adult males, 0·259 mg. ; and females, 0·256 mg. The minimum dry weights were for Stage V, 0·078 mg. (1st October) ; for adult males, 0·100 mg. (16th October) ; and for females, 0·100 mg. (16th October and 26th November).

TABLE I.

RAW WEIGHT IN MILLIGRAMS.

Months.	February.			March.			April.	
Dates.	12	19	26	5	12	27	11	16
V	0·40						0·44	0·48
VI ♂	0·58	0·61						0·64
VI ♀	0·69	0·58	0·56	0·78	0·59	0·58	0·64	0·89

Months.	May.			June.			July.		August.
Dates.	7	15	22	10	19	26	4	9	7
V	0·70	0·68	0·62	0·50	0·66	0·43		0·57	0·55
VI ♂	0·85	1·13	0·90	0·69	0·74		0·74	0·74	0·72
VI ♀	1·05	1·10	1·10	0·84	0·93	0·80	0·86	0·88	0·89

Months.	September.		October.		Nov.	December.			
Dates.	3	16	14	16	13	3	10	17	22
V	0·61	0·39	0·35	0·40	0·35	0·45	0·39	0·40	0·39
VI ♂	0·83		0·73		0·50	0·55	0·59	0·55	0·53
VI ♀	0·93	0·81	0·53	0·41	0·50	0·56	0·62	0·55	0·48

TABLE II.

Dry Weight in Milligrams.

Months.	February.			March.		April.		May.		
Dates.	12	19	26	5	27	11	16	7	15	22
V		0·132				0·116	0·119	0·248	0·252	0·216
VI ♂		0·128					0·158	0·256	0·259	0·250
VI ♀	0·100	0·122	0·118	0·130	0·138	0·126	0·175	0·254	0·256	0·252

Months.	June.			July.		August.	September.	
Dates.	10	19	26	4	9	7	3	16
V	0·150	0·190	0·166	0·184	0·196	0·196	0·134	0·139
VI ♂	0·184	0·206		0·200	0·174	0·154	0·170	0·163
VI ♀	0·186	0·224	0·172	0·172	0·214	0·214	0·210	0·177

Months.	October.			November.		December.			
Dates.	1	14	16	13	26	3	10	17	22
V	0·078	0·116	0·112	0·128	0·116	0·106	0·128		0·138
VI ♂		0·120	0·100	0·110		0·118	0·141	0·131	0·109
VI ♀	0·134	0·110	0·100	0·124	0·100	0·110	0·126	0·120	0·141

TABLE III.*

Median Length (Q_2) in Millimetres.

Months.	February.			March.			April.		
Dates.	12	19	26	5	12	27	11	16	24
V		2·72					2·89	2·98	
VI ♂	3·01	3·02					3·30	3·27	
VI ♀	2·98	2·98	2·97	3·00	2·96	2·98	3·07	3·40	3·53

Months.	May.			June.			July.		August.
Dates.	7	15	22	10	19	26	4	9	7
V	3·15	3·09	2·96	2·88	2·86	2·75	2·86	2·81	2·84
VI ♂	3·54	3·59	3·52	3·30	3·30		3·20	3·14	3·19
VI ♀	3·57	3·58	3·61	3·37	3·37	3·27	3·24	3·25	3·30

Months.	September.		October.			November.		December.			
Dates.	3	16	1	14	16	13	26	3	10	17	22
V	2·85	2·75	2·67	2·61	2·69	2·74	2·67	2·56	2·70	2·63	2·75
VI ♂	3·24	3·14	2·95	2·80	2·84	2·90	2·85	2·98	3·09	3·01	2·99
VI ♀	3·38	3·24		2·93	2·83	2·90	2·84	2·94	2·87	2·90	2·85

From the measurements for Stages V and VI males and females were calculated the quantities Q_1, Q_2, and Q_3, Q_2 being the median size (see Tables III and V, and Fig. 3).

Stage IV was very scarce owing to the large-meshed net employed. Measurements gave the following results: April 11th, 2·28 mm. and 16th, 2·07 mm.; May 7th, 2·39 mm.; June 10th, 2·10 mm.; July 4th, 2·10 mm.

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* In the table are not included data of days when quantity of sampled material was too small to allow computation of average size (Q_2).

and 9th, 2·13 mm.; September 16th, 2·15 mm. and 24th, 2·20 mm.; October 1st, 2·06 mm. and 14th, 2·11 mm.

The maximum average length of the body occurred in May: Stage IV, 2·39 mm.; Stage V, 3·15 mm.; Stage VI males, 3·59 mm.; and Stage VI females, 3·61 mm. The minimum average size occurred in October: Stage IV, 2·06 mm.; V, 2·61 mm.; VI males, 2·80 mm.; VI females, 2·83 mm.

In spite of the great changes of biomass and size during the year we see that for certain periods (see Figs. 2, 3, and 4) both biomass and size remain nearly constant. Three such seasons may be observed:

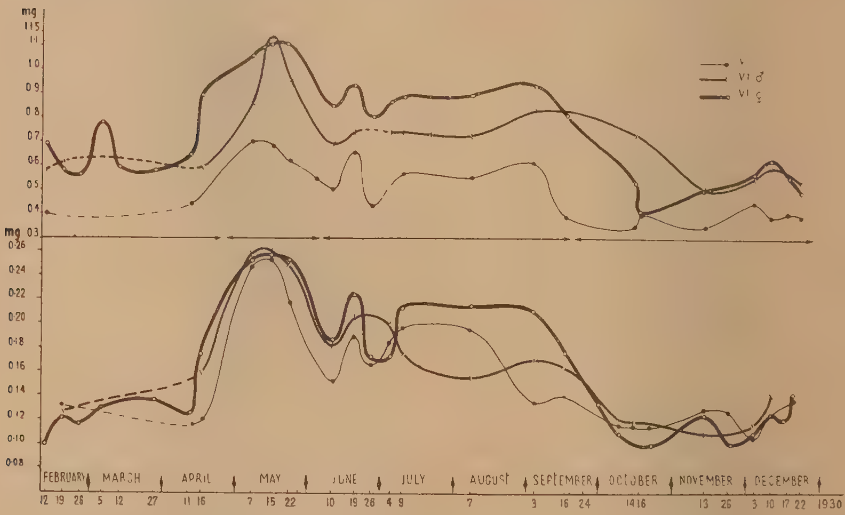

FIG. 2.—Seasonal changes of biomass in *Calanus finmarchicus* (copepodite Stages V, VI males and females) in the Plymouth area in 1930.

Upper part of the graph—curves for variations in average raw weight. Lower part of the graph—curves for variations of average dry weight. Horizontal line with arrows—period of predominance of a given generation.

The first season—"autumn–winter"—from end of September to middle of April; the second season—"spring"—from end of April to June; the third—"summer"—from June to middle of September. As may be seen the seasons differ greatly in duration; and do not coincide with calendar seasons. But yet they are well differentiated in the biomass and size of Calanus. Small fluctuations in the curves during each season are possibly due to faulty methods in preparing and sampling of material.*

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* Marshall (1933) has since shown that this may possibly be due to differences in size between the first and last born in any generation, the former being slightly larger than the latter.

The length of the season is given in Figure 2 by horizontal lines. Our seasons may also be well characterized from the hydrographic view-point (Harvey, 1930) especially according to temperature. The "autumn-winter" season is characterized by homogeneousness of temperature from surface to bottom, the temperature value decreasing from month to month. Towards the end of the "spring" season a discrepancy appears between surface and bottom temperature, that of the surface getting warmer. The "summer" season is characterized by a marked stratification of temperatures and a strong warming of the whole mass of water.

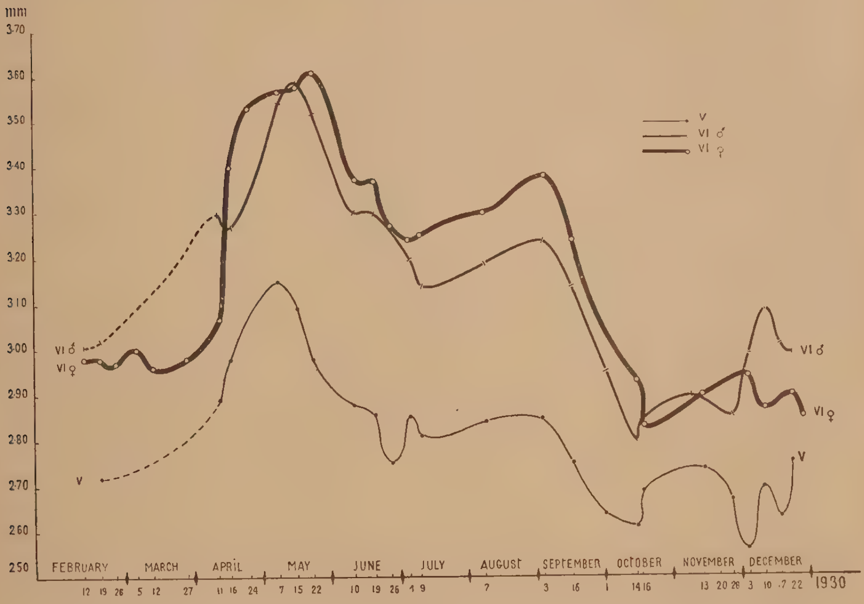

FIG. 3.—Seasonal changes in average size (Q_2) of *Calanus finmarchicus* (copepodite Stages V, VI males and females) in the Plymouth area in 1930.

especially of the surface layers, the warmest time being towards the end of August and the bottom water attaining its maximum in September.

The salinity in the Plymouth area is subject only to slight fluctuations, its value being about 35°/₀₀. The main source of the water supplied to the English Channel is the Atlantic. In the course of the year the main current of the English Channel is unstable in strength and partly in direction.

To characterize our seasons by biomass and size I have summed up data of Tables I, II, and III. In this way I obtained the following average values for biomass and size (Table IV) :

TABLE IV.

	Stages.	Seasons. Autumn, Winter.	Spring.	Summer.	Yearly average.	Ratio of Spring/ Autumn-Winter.
Raw weight mg.	V	0·40	0·67	0·53	0·53	1·7
	VI males	0·59	0·98	0·74	0·77	1·66
	VI females	0·60	1·08	0·87	0·85	1·8
Dry weight mg.	V	0·117	0·239	0·169	0·174	2·04
	VI males	0·124	0·255	0·179	0·186	2·06
	VI females	0·123	0·254	0·196	0·191	2·06
Average size mm.	V	2·72	3·07	2·82	2·87	1·13
	VI males	3·00	3·57	3·22	3·26	1·19
	VI females	2·96	3·57	3·30	3·28	1·21

Stage IV, which was very scarce, is not included in this table. The table shows that the minimum of biomass in the " autumn–winter " season is about as much smaller than the yearly average as the maximum of the " spring " season is greater. Values characteristic for " summer " forms are approximately equal to the yearly average.

The picture of the change in biomass and size during the year is as follows : Early in the year (from February to mid-April) the biomass and size are small. In April the picture begins to alter and in the material of April 16th occur big forms (see Fig. 4) and we observe a decided rise of the average for biomass and size. The big organisms prevail from the end of April and throughout May, the average value of biomass and size being at its maximum, which is characteristic for our " spring " season. From the end of May (May 22nd) begins a decrease in biomass and size, slight for adults and considerable for Stage V, continuing to the first decade of June. During the subsequent months, to the middle of September, the values of biomass and size remain stable, which is characteristic for our " summer " season. From the middle of September for adults, and the end of August for Stage V, biomass and size begin to decrease, the values reaching their lowest level in October and slightly rising again in the subsequent months, but still being very low and deviating greatly from those of the " spring " and " summer " seasons, which is characteristic for the " autumn–winter " season, from end of September to the middle of April.

August and September are intermediate months (see Fig. 4) containing forms, characteristic for different " adjacent " seasons, some organisms gradually replacing others in the course of the month. Evidently the same may be expected in June, but here the replacing of " spring " organisms by " summer " ones is much more rapid and does not show clearly in our material.

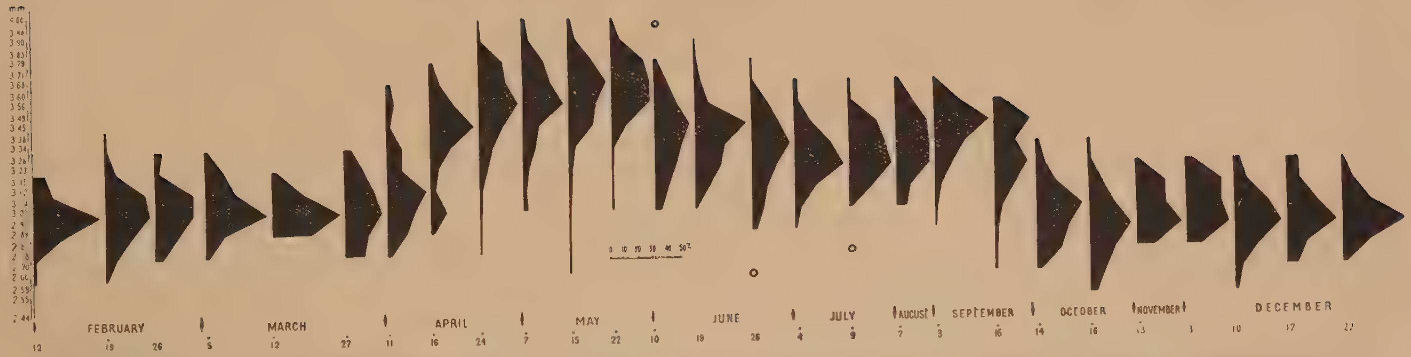

Fig. 4.—Seasonal changes in the percentage size distribution of *Calanus finmarchicus* (Stage VI females) in the Plymouth area in 1930.

In the curves for "dry weight" (Fig. 2) we see the stage-curves following one another very closely. This shows that the difference in "raw weight" between Stage V and adults is due to the difference in quantity of water in specimens of these two stages. Calculation has shown that the surplus of raw weight over dry weight is not constant throughout the year or for different stages. Below are given data showing the ratio of raw weight to dry weight. (The figures show how many times raw weight is greater than dry weight.)

	Seasons.			
Stages.	Autumn–Winter.	Spring.	Summer.	Yearly average.
V	3·40	2·80	3·10	3·10
VI ♂	4·75	3·80	4·10	4·22
VI ♀	4·90	4·20	4·40	4·50

These figures show that the adults contain more water than Stage V, the greatest quantity being in females (VI ♀), and that during the "autumn winter" season the quantity of water is at its maximum, the minimum occurring in the "spring" season. If the quantity of water be expressed in percentages, it shows (yearly average data) that Stage V contains 65% of water; adults VI males, 76%; and VI females, 78%.

DISCUSSION.

No exhaustive data have been published on the biology of *Calanus finmarchicus* in the Plymouth area. Gough (1905), Lebour (1917), and others record the presence of *C. finmarchicus* all through the year and its predominance (Lebour, 1917) from the end of April to the beginning of November. Russell (1928) was the first to give quantitative data for Calanus in the Plymouth area (Stage V and adults, males and females) for a period from April 9th to September 22nd, 1926. His results show that the adults exhibit two maxima in abundance, the first in May-June, the second in August. Stage V shows an alternating decrease and increase in quantity each month.

Russell (1933, Table I, p. 76) gives the total numbers of Calanus in the half-hour oblique hauls from which my material was obtained, and these results are plotted in Figure 5. Early in the year *C. finmarchicus* was very scarce. In March Stages V and VI♂ were entirely lacking. At the beginning of April the quantity began to increase rapidly showing enormous figures to the end of the month. In May the quantity increased still further, reaching on May 7th the maximum of 318,450 specimens in a half-hour haul. In June the quantity shows a marked fall, still remaining at a comparatively high level (about 1000 specimens for a half-hour haul) and keeps stable during the whole summer to the beginning of August. From the end of September the number begins to decrease rapidly (about 100 specimens per haul) becoming quite small in the middle of October and remaining so through all the "autumn–winter" period. There are occasional marked decreases in quantity, e.g. at the end of April, or in summer, but the general trend of the curve remains constant.

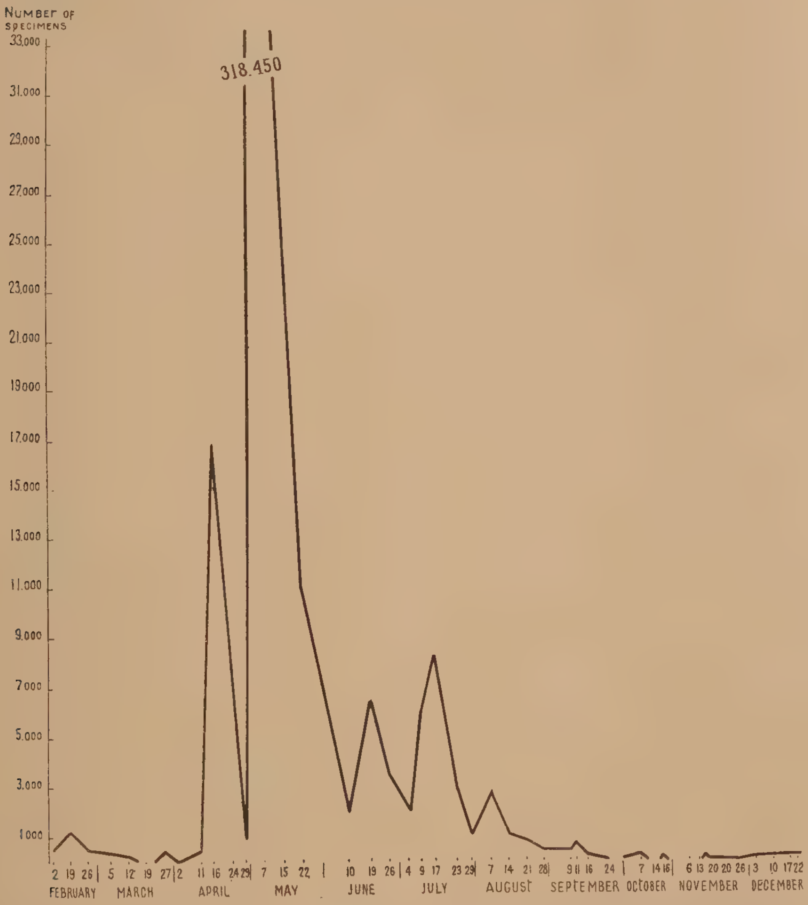

FIG. 5.—Seasonal changes of total number of *Calanus finmarchicus* (copepodite Stages IV, V, VI—males and females) in the Plymouth area in 1930.

Number of specimens caught during a half-hour oblique haul with a 2-metre stramin ring-trawl. Mostly composed of Stage VI females.

The same picture is given by other authors for different parts of the North Sea and the adjoining areas: Paulsen (1906), Damas (1905), Gran (1902), Marshall (1924), Farran (1920, 1927), Johnstone, Scott, and Chadwick (1924), Runström (1932), and others.

The observed times of reproduction of *Calanus finmarchicus* in different parts of the North-European seas are as follows :* Gran (1902) states that the period of reproduction is April–May for the North-Western coast of Norway ; Damas (1905), June for the Norwegian Sea ; May and June for the Faroe Islands. Paulsen (1905), from the end of March up to June for Southern Iceland. Damas and Koefoed (1907), end of June for Norway and Spitzbergen. With (1916), June for Danish current ; May, for Southern Iceland ; June and July, for Western Greenland, and the end of June for Eastern Greenland. Johnstone, Scott, and Chadwick (1924) assign the time from June to August and from September to October as the periods of reproduction for the Irish Sea in the area of Port Erin, whilst Farran (1927) considers April and May as the main period of reproduction for the given area.

The occurrence of both males and females of *C. finmarchicus* all the year round in these regions gives rise to the suggestion that there may be several periods of reproduction and hence several generations in the course of a year.

Paulsen (1905) suggests two periods of reproduction for Iceland area : early spring and end of summer. Ruud (1929) points out the occurrence of a great number of nauplii in the Möre area in March–April and June–July, indicating that there may be two periods of reproduction in this area, in spring and in summer ; the suggested time of spawning for the first period is February–March, for the second, May–June.

In Runström's (1932) tables on page 58-59 we see that the great quantities of *C. finmarchicus*, occurring from March to September, are interrupted by smaller quantities in July. This may be explained by the existence of two periods of reproduction.

Russell (1928) on the basis of measurements states that the great number of *C. finmarchicus*, appearing at the end of April, were hatched in March. This brood is marked by its large size and is termed by the author as " large " brood. This " large " brood is short-living and in the course of May reproduces individuals of a smaller size, " small " brood, and soon dies off. Throughout the summer months, July and August and presumably in September, intermittent spawning occurs, resulting in a new generation, which tides over the winter months to spawn early in the next spring and reproduce once more a brood of large individuals. Females carrying spermatophores occur throughout the year ; in April the number of spermatophore-carrying females is greater than in the following months of May and beginning of June ; then it rises again, reaching the April value in August.

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* Most authors have no yearly material available, which is a drawback.

Thus we may consider that Russell records three periods of reproduction throughout the year, the first period being March–April ; the second, May ; and third, July–August.

In other regions, too, several periods of reproduction are recorded. Bigelow (1926) records two periods of reproduction for the area of the Gulf of Maine—spring (May) and autumn (September). The first period gives rise to abundant masses of *C. finmarchicus* in spring and summer months ; the second period gives smaller quantities, but constantly occurring in the winter months and reproducing again great quantities in spring.

Farran (1927) finds that in the area south of Ireland the young of the previous year become adult in January, February, and March, and that there is a big outburst of reproduction in March–April, reproduction then going on irregularly throughout the rest of the summer.

We have the right to presume the existence of only one generation for Arctic seas, where males occur in a definite short period of time, being quite rare in the plankton (Bogorov, 1932) ; whereas in those regions, where both sexes occur throughout the year, we have full reason to presume the existence of several periods of reproduction.

My Plymouth material, though not supplying data on young stages and on the presence of spermatophore-bearing females, leads me, nevertheless, to conclusions approaching those of Russell ; I endeavoured to complete these data with winter material and to complete the picture of yearly changes in the biomass.

Taking the period of development of Calanus from egg to adult as averaging two months (Lebour, 1916), the rate of the process being different at different seasons, we may presume that the appearance of great masses of Calanus at the end of April and especially in May is due to their reproduction early in the year. These individuals differ appreciably in size and weight from those occurring in winter catches (see Fig. 4). They are considerably greater and heavier ; VI females, size, 3·57 mm. ; raw weight, 1·08 mg. ; dry weight, 0·254 mg. (see Table IV), whereas the size and weight of the " autumn–winter " individuals, having produced the above mentioned is : VI females, size, 2·96 mm. ; raw weight, 0·60 mg. ; and dry weight, 0·123 mg. The generation of big individuals predominates in the adult stage for a very short time, from end of April to beginning of June, after which, as Figure 4 shows, it disappears, giving place to smaller and lighter individuals, resulting from a generation, produced from big individuals of the end of May. This new generation predominates from June to the beginning of September and is characterized by its size : VI females, 3·30 mm. ; raw weight, 0·87 mg., and dry weight, 0·196 mg. In September occurs a rapid disappearance of the generation in question, and a replacement by smaller individuals. The latter generation results from intermittent reproduction throughout the summer season, as pointed out by Russell.

It may be supposed that the end of August and beginning of September is the last period of summer reproduction, the resulting generation tiding over the autumn–winter period. Such intermittent reproduction makes both biomass and size unstable in the autumn and winter periods. However both biomass and size show a slight marked tendency to increase in the course of the period. This is clearly shown by changes in the monthly average.

Stage.	Raw weight.					Dry weight.					Size.				
Months.	Oct.	Nov.	Dec.	Feb.	Mar.	Oct.	Nov.	Dec.	Feb.	Mar.	Oct.	Nov.	Dec.	Feb.	Mar.
V	0·38	0·35	0·41	0·40		0·102	0·122	0·124	0·132		2·66	2·71	2·66	2·72	
VI ♂	0·73	0·50	0·56	0·60		0·110	0·110	0·125	0·128		2·86	2·88	3·02	3·02	
VI ♀	0·47	0·50	0·55	0·61	0·65	0·115	0·112	0·124	0·113	0·134	2·88	2·87	2·89	2·98	2·98

Hence biomass and size in February and March are greater than in October, November, and December. This is probably due to the dying-off of the early born individuals; Stage V being the source from which adults are drawn (recorded by Farran, 1927) up to the end of February, at which time all the Stage V pass into adults. This coincides with the disappearance of adult males, and supports the suggestion that fertilization had taken place not long before, after which appears a new generation. Several months may elapse before the laying of eggs and hatching of nauplii as pointed out by Farran (1927).

It is worthy of notice that during the " autumn–winter " season males are much more abundant than females, which is just the reverse in other periods.

We would be justified in considering the *C. finmarchicus* of different sizes occurring at different seasons as separate generations if we had proof enough that they actually originated from one another, and that the waters of the region investigated were of the same origin. To decide the first question we need information on the occurrence of the different stages of development throughout the year (viz. eggs, nauplii, and all copepodid stages). Unfortunately I have no available material of that kind, but the literature data, especially those supplied by Russell (1928) and the hydrographical conditions of the waters of the English Channel, strongly support the opinion that several generations may occur here, the waters being from a homogeneous source, namely, the Atlantic.

For lack of material I can give no definite answer to the essential question, whether the Calanus in the Plymouth area are constant inhabitants or whether they are brought here by water currents. But even if these masses of Calanus are brought from another region, our considerations hold true and we have only to make allowance for the time of migration of these masses and for the areas of reproduction of Calanus, from which the main source of supply in the Plymouth region is drawn.

As a result of the present investigation we have the following " generations," which I have named according to the seasons in which they predominate.

The " spring " generation—resulting from reproduction in February–March. Adults predominate in the plankton for about a month and a half (from end of April to May). Value of biomass and size is greatest compared to that of other seasons (Table IV, Figs. 2 and 4).

The " summer " generation—resulting from May reproduction. Adults prevail for about 3½ months from June to mid-September. In biomass and size they are smaller than those of the spring generation.

The " autumn-winter " generation—resulting from intermittent reproduction during the summer months from June to August. The adults prevail during eight months from end of September to mid-April. In biomass and size this generation is the smallest.

What are the causes of seasonal changes of biomass and size ? In Figure 6 are given changes in temperature (from Russell, 1932) and in the size of Calanus for the year 1930. The salinity in the Plymouth area is not subject to any appreciable changes in the course of the year ; the source of water supplied into the Channel remains the same, namely the Atlantic.

While it must be realized that many factors influence biological phenomenon it is evident that temperature is of great importance, reflecting as it does, other environmental changes.

Considering the two-months period, which Calanus takes for developing from the egg to the adult, we see that the " spring " Calanus hatched and developed in cold winter water at the temperature of 8-9° ; the " summer" Calanus grew up in the warmer water of spring and early summer at 10·5–14·5° ; and the " autumn-winter " Calanus developed in still warmer water of the end of summer at 15–16° C. Plotting on the same graph (Fig. 6) the curve of change of biomass, characteristic for the given season (Table IV) and that of temperature conditions characteristic for the moment of reproduction and beginning of development, i.e. two months previously, we obtain evidence of the interrelation between temperature conditions at the beginning of development and the value of biomass and size of the adults. We see that big organisms with large biomass and size are generated under low temperature conditions and *vice versa.* If we follow the changes in biomass and size during the " autumn–winter " season we observe, as stated above (page 600), that the value of both increases from month to month, the temperature falling respectively. Again we see here the same interrelation, i.e. falling of temperature producing increase in biomass and size.

In contrast to the above we have to deal here with the long-living Stage V, which gradually passes into the adult stage (as recorded by Farran, 1927). Resulting from such lengthy development under conditions of continually decreasing temperature we obtain, in February–March, organisms marked by their greater size in comparison with individuals of the same generation, which have passed a shorter cycle of development and reached the adult stage in October–December. Thus the influence of temperature, which affects later stages of development, is noticeable in the size of adult organisms just as much as if it had occurred in earlier periods of growth.

Investigations on the yearly changes in size of marine and fresh-water copepods have been made by a number of workers; amongst these the following may be quoted, Adler and Jespersen (1920), on Calanus, Pseudocalanus, and Temora; Gran (1902) on Calanus; Rzoska (1927) on *Cyclops strenuus*; Störmer (1929); Ruud (1929); Gardiner (1933); and Russell (1928) on Calanus.

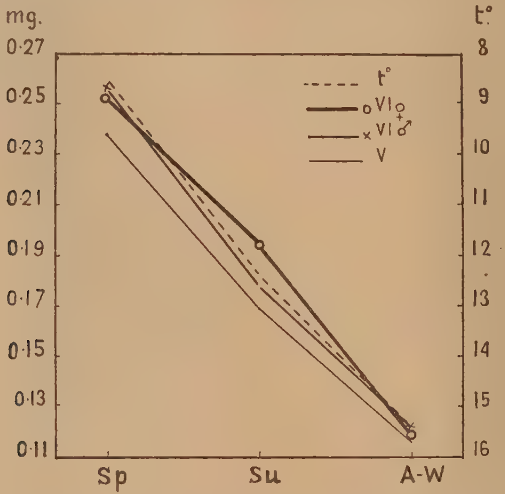

Fig. 6.—Average biomass of a generation of a given season; temperature at time of hatching and beginning of development of a given generation. Sp. = Spring; Su. = Summer; A.–W. = Autumn–Winter.

Comparing our results of 1930 with those of Russell (1928) for 1926 we plotted a graph (Fig. 7) where the thick line shows our results and the thin one those of Russell. We see that in the main 1930 results are characterized by lower temperature and greater size while in 1926 we observe the reverse phenomenon. The graph as a whole, as well as in detail, is very convincing. The "spring" Calanus of May 1930 is larger than that of

1926, temperature conditions at the time of hatching and development (February–March) in 1930 being colder than in 1926. In June and beginning of July the size-curves of 1930 and 1926 follow one another very closely, showing even a smaller size in 1930, but the temperature conditions of May, when the generation in question was developing, were warmer in 1930 than in 1926. Further, the summer of 1930 was colder than in 1926, resulting in the greater size of Calanus of 1930. Finally, in early autumn the temperatures of 1930 and 1926 become similar, which is reflected in the close coincidence of the curves.

It is interesting that the size-curve of summer 1930 is repeated as it were by the temperature curve. Thus we see that the forms in September are larger than those in July. This discrepancy with the basic data is not essential as far as biomass (Fig. 2) is concerned, and the sizes of 1926 Calanus do not exhibit such a picture. It is worthy of notice that the discrepancy between the sizes of 1930 and those of 1926 at the same time is as great as the difference in temperatures of June and early July, which fact, considering the time of development of *C. finmarchicus*, is another proof of the definite dependence between temperature and size of organisms.

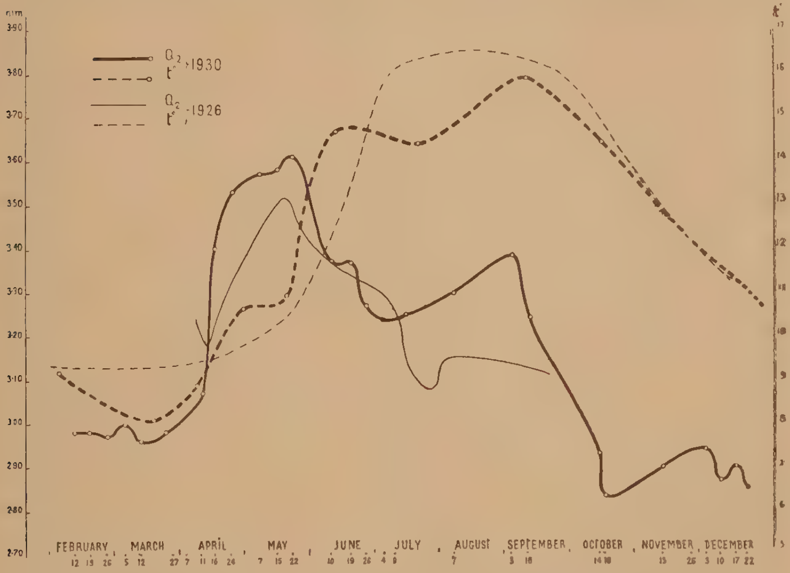

Fig. 7.—Comparison of seasonal changes of size of *Calanus finmarchicus* (Stage VI females) and of temperature in the years 1930 and 1926 in the Plymouth area.

Thick line, 1930; thin line, 1926; continuous line, size of females; broken line, temperature.

In order to elicit the correlation of temperature and size of organism I drew a correlation table (Fig. 8), (*a*) for comparing the biomass and length of organism and the temperature of the medium (Nos. 1 and 3), this being the static moment; and (*b*) for comparing the temperature of the period of reproduction with the biomass and length of the resulting generation (Nos. 2 and 4), this being the dynamic moment. In order to

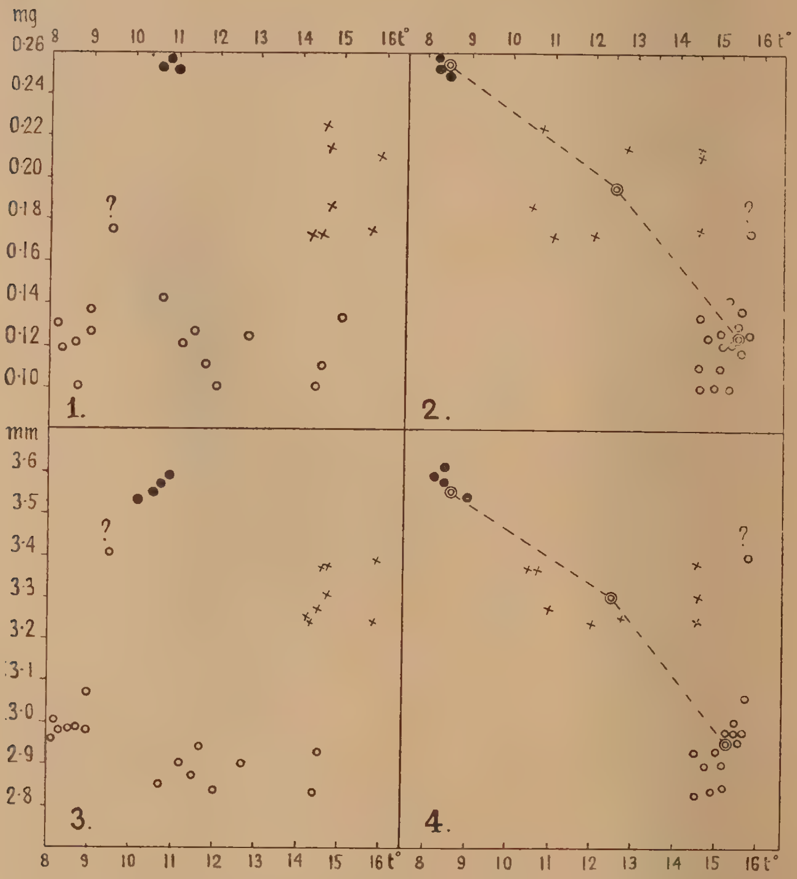

FIG. 8.—Correlation table. Comparison of size and biomass of *Calanus finmarchicus* (females) with temperature.

Nos. 1 and 3—Comparison of biomass (dry weight) and size with temperature of medium. Nos. 2 and 4—Comparison of biomass and size with temperature at time of hatching of given generations.* (● =Spring generation ; × =Summer generation ; ○ =Autumn–Winter generation.)

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* In Nos. 2 and 4, average values of a given generation are connected by a straight line.

facilitate reading I have put different signs for different generations. The correlation table shows clearly that firstly (Nos. 1 and 3) small and large organisms occur at all possible temperatures, and secondly (Nos. 2 and 4) all points are strictly within definite temperature limits ; if a line be drawn from small to large organisms it will show that low temperature throughout the period of development is the greatest stimulant to growth and *vice versa.*

The graph shows also that in studying the correlation of temperature and size the question is to be regarded from the point of view of dynamics.

A number of investigations on origin of forms in Copepoda show that different geographic-hydrological areas are inhabited by different species and more minute taxonomic subdivisions, low temperature areas being characterized by species and forms of larger size, whereas the warm tropical waters are inhabited by small-sized forms. In a series of papers Steuer (1923 and 1931) has shown on the genus Acartia, Pleuromamma, and Rhincalanus that, for example, the large-sized species *Rhincalanus gigas* is abundant in the cold waters of the Antarctic. The medium-sized *R. nasutus* is widely known in all oceans, but in the colder waters. The small-sized *R. cornutus* is met with in the warm surface water of the Atlantic and Indian Oceans.

By comparing the size of *C. finmarchicus* in the Barents Sea with that of this species in the Plymouth area I found (1933) that the former was much larger. The temperature conditions of Barents Sea waters are much colder than those of the Plymouth area, which accounts for the difference in size of the Calanus.

Many of the above-mentioned authors—Adler and Jespersen (1920), Ruud (1925), Störmer (1929), and others—give the same data. Later investigations in Barents Sea (Bogorov and Preobrajenskaya) have shown, that in different areas of the Barents Sea, which is heterogeneous in its hydrographical conditions, both biomass and size of *C. finmarchicus* vary also, being larger in cold-water than in warm-water regions.

It would be interesting to make an attempt to find the interdependence between biomass of the plankton organism and the temperature differences.

The difference in temperature between the times of hatching of " spring " and " autumn–winter " generations of *C. finmarchicus* in the Plymouth area is about 8°. In biomass the " spring " Calanus are twice as large as the " autumn–winter " ones. The difference of temperature of the English Channel and the Barents Sea* is about 10° ; average biomass in *C. finmarchicus* of the Barents Sea is about twice the value of that of *C. finmarchicus* in the English Channel. But the comparison of the northern part of the Barents Sea with the southern one showed that 5° difference in temperature brought forth a threefold difference in biomass. Hence the value of the difference in temperatures depends on its place on the temperature scale, the influence of smaller differences in temperatures, under lower temperatures having a greater effect than large differences at higher temperatures. This means that the size of an organism (biomass) is no simple function of one single factor, even if it be such an important one as temperature, and that there is in different cases the combined influence of various conditions, forming altogether the physico-chemical and biological complex of conditions of existence of the organism. It is quite evident, nevertheless, that temperature conditions are of paramount importance in this complex.

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* In both cases we compare the temperature for time and locality of sampling of *C. finmarchicus*, hence our average data are not the averages for the whole English Channel or the Barents Sea.

We stated above that the *C. finmarchicus* of the Barents Sea produces only one generation in the course of the year while that of Plymouth area gives three generations. Thus the Calanus of the Barents Sea lives longer than that of Plymouth area, its biomass also being respectively greater. This leads to the conclusion that organisms in cold-water regions have the advantage of greater biomass, whereas warm-water organisms can produce more generations. It is interesting to note that when summed up, the biomass of three generations of *C. finmarchicus* in the Plymouth area (adult females –2·55 mg. raw weight and 0·574 mg. dry weight) approximately equals the average biomass of Calanus in the Barents Sea (adult females—2·18 mg. raw weight, 0·670 mg. dry weight).

These results lead up to the general problem of the relations between temperature, development, and length of life, feeding and metabolism, and growth in size. Amongst others the following workers may be cited: Rzoska (1927) on Cyclops; Russell (1932) on Sagitta; Mielck (1919, cited from Samojloff, 1926) on Arctic fishes; Loeb (1910); and Adler and Jespersen (1920). No decisive answer, however, can be found until we know exactly the quantitative and qualitative variations in the food consumed throughout the year. The food of Calanus has been investigated by Marshall (1924), but in insufficient detail for our purpose. It is interesting that the spring and summer Calanus are reddish yellow with abundant fat inclusions, while the winter specimens are greenish white, and lacking fat inclusions or with very slight ones, presumably due to reduced winter nutrition. Samojloff (1926) has suggested a knowledge of the age to which fossil animals lived will help towards obtaining the temperature conditions of bygone times.

Before concluding I should like to emphasize one particular point I recorded above that the maximum number of specimens fell in with the maximum value of biomass and sizes in spring and *vice versa*, the minimum quantity occurring during the period of the minimum of biomass and size in autumn and winter. This is clearly seen from the details; thus in June (Figs. 2 and 5) we observe, as it were, a pulsation of quantity, reflected by a similar pulsation in biomass—greater biomass and greater number of individuals occurring simultaneously. I suppose this must be explained by the fact that conditions, favourable for the rise in biomass, are at the same time optimal ones for the development of great numbers of individuals. This result is of great biological importance, being contrary to the generally accepted view that the larger-sized organisms are more easily formed in regions with scarce population, where the density of life (number of individuals per definite volume) is smaller.

All the factors mentioned affect to some greater or smaller degree the size of an organism dependent on different combinations of life conditions and forming in their complex the essential problem of " organism and medium." In this complex of various conditions the temperature is the most important, biomass and size of organism being reversed in proportion to temperature conditions during the time of growth.

SUMMARY.

1. The present paper deals with changes of biomass and size of *Calanus finmarchicus* throughout the year in the Plymouth area.

2. The material was supplied by regular oblique hauls during 1930; Stage V and adult males and females having been examined. *Calanus finmarchicus* occurred throughout the year reaching its maximum value in May, being abundant from the middle of April to the middle of September.

3. *Methods.* The study of the material was based on the determination of *raw weight*, *dry weight*, and *length measurements*. For determination of *raw weight* a special method was worked out consisting of " liquid " drying of the body surface with alcohol and ether flowing through a special device, air being pumped through eventually for driving away the ether vapour. This method supplies data more suitable for comparison than those obtained by filter-paper drying. *Dry weight* was determined after drying in a desiccator. The data of *dry weight* are more exact and reliable than those of *raw weight;* dry weight also gives a better idea of quantity of substance, i.e. biomass of the plankton organism. *Raw weight* depends chiefly on the quantity of water in the organism.

Total length of the body was determined.

4. In the course of the year both biomass and size vary appreciably, the size of an organism being, however, approximately constant for a given period of time. Three such seasons are adopted; the first—" spring "

season—May; the second "summer" season—June, July, August, September; and the third—"autumn–winter"—from October to April.

5. These seasons are markedly differentiated in biomass and size, which are characteristic for each season (see Table IV): thus the maximum biomass for all stages occurs in the spring season, decreasing in the summer season and reaching then the yearly average. In the autumn–winter season we have the minimum biomass. Size varies similarly.

6. For the area under investigation we think it possible to specify three periods of reproduction, hence three generations of *Calanus finmarchicus*, named in respect to their time of living "spring," "summer," and "autumn–winter."

The length of life of each generation depends on the length of a given hydrological regime, a new generation growing up at the time of basic change in the regime, the old one dying off.

7. A definite relation is obvious between size of organism and hydrological conditions, the main factor being temperature, particularly during the period of development. Thus the large sized "spring" generation was hatched at 8–9° C. of temperature; the smaller-sized "summer" generation at 10·5°–14·5° C.; the very smallest "autumn–winter" hatched at the warmest temperature of 15–16° C. (see Figs. 7 and 9). We are justified in presuming that the size attained and the temperature conditions during development are inversely proportional.

8. Interrelation between temperature and size of Copepoda has been recorded by many authors, size being largest at low temperatures and *vice versa*. This phenomenon is widely known and used in comparisons of all kinds: geographical, regional, seasonal, vertical (from surface to bottom), sectional (crossing water with different temperature conditions), yearly (comparing years having different temperature conditions).

9. Generations differ from one another not only in size but in physiology (F. S. Russell).

10. Data of dry weight show that the body of adult females contains a greater percentage of water, the water-content varying with seasons, being at its minimum in spring and reaching the maximum in winter.

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TABLE V.

Measurement of Total Length of Female Calanus (Stage VI ♀) in Millimetres, 1930.

mm.	February 12	February 19	February 26	March 5	March 12	March 27	April 11	April 16	April 24	May 7	May 15	May 22	June 10	June 19	June 26	July 4	July 9	August 7	September 3	September 16	September 24	October 1	October 14	October 16	November 13	November 20	December 3	December 10	December 17	December 22
4·00												1																		
3·97									1																					
3·94										1	1	1	1																	
3·90									1		2																			
3·86									2	2	3	8		1																
3·83									2	4	9	7																		
3·79									8	3	12	8																		
3·75								2	13	8	23	23	1	1																
3·71								1	5	6	15	14	1	2	1															
3·68								2	10	8	26	25	4	3		1		1	1											
3·64								3	14	7	22	10	3	1		1			1											
3·60							1	5	19	8	30	18	3	2	1	5	2	3	1											
3·56								7	25	16	29	28	5	4	2	2	2	9	8	1										
3·53							2	6	19	8	13	17	10	5	4	1	1	8	11	2										
3·49								10	18	10	16	8	3	3	5	5		8	12	3										
3·45								14	15	5	14	10	9	9	4	5	6	17	23	5		1								
3·41							1	15	10	5	16	6	6	10	3	13	6	19	29	5	1									
3·38		1						16	13	3	21	7	14	25	14	12	12	12	21	13										
3·34			1				4	8	9	7	5	1	9	8	4	16	9	23	13	5			1							
3·30				1		2		8	7	3	7	1	10	11	7	22	11	16	18	6			1							
3·26		2	2	1				3	5		3	1	3	6	16	22	10	12	11	3			1					1		
3·23		1		3	1	1	1	2	5	1	2	1	9	9	8	37	12	20	13	9	1	1	2	1						
3·19	1	5	1	3		1	1	6	3	3	5		3	7	3	22	13	18	8	4			5	1	1	1	1	1	2	1
3·15	2	2	1			3	2	1	5	1	1	1	5	5	7	21	9	13	4	8	2	2	1				2	2	4	
3·12	1	9	3	1		2	3	1	2	2	1	1	3	2	6	9	10	6	6	2		2	5	1			5	2	1	1
3·08	3	11	2	1	3	3	5	3			2		5	2	2	15	5	8	3	8		2	9	1	2		2	2	4	2
3·04	1	8	10	7	2	3	2	1	2		2	1	1		3	12	6	7	2	3		1	4	4	6		5	1	2	1
3·00	6	10	6	9	4	3	3	5	1	1	2	1	2		5	7	1	9	1	4	1	1	9	5	3	1	5	6	8	5
2·96	3	8	5	4	2	2	1	7	1				2	1	2	4		4	3	1	1	1	10	3	1		2	3	8	3
2·93	7	13	4	5	5	5	3	2	2	2			1		1	1	2			1			13	5	4	1	5	5	5	2
2·89	2	5	3	1	4		2	1	1		1				3				3	1		1	5	5	4		4	6	6	5
2·85	1	8	13	1	1	3		1			2					1				1	1	2	13	6	3	2	4	8	13	7
2·81	4	6	2	4	1	3	3									1				1		1	7	9	5	2	6	9	4	10
2·78		2	1			2															1	1	9	8	2	1	3	2	2	2
2·74		4	1	1		3			1											2			6	3	1		1	4	3	3
2·70	1	2	1			1	1				1						1				1		5	2	2		1	4	5	5
2·66	1																			1	1		3	2		1		2	2	1
2·63		1									1				1					1			2	4				1	1	1
2·59																							1	2		1		1	2	
2·55																								3				1		
2·52																									2					
2·48																														
2·44																									1					
2·40																														
Total number	33	98	56	42	23	36	35	130	219	114	287	199	113	117	102	235	118	213	192	90	10	16	112	66	37	9	46	61	72	49

On the Biology of *Calanus finmarchicus.* Part IV. Seasonal Changes in the Weight and Chemical Composition in Loch Fyne.

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With 5 Figures in the Text.

THE value of the zooplankton as a fish food depends not only on its distribution and numbers but also, to a large extent, on its chemical composition. Analyses of the marine plankton have already been made by Brandt (1898), Brandt and Raben (1919 22), Meyer (1914), Moberg (1926) and Wimpenny (1929). These authors worked on tow-nettings containing mixed plankton, both plant and animal. In the analyses of Brandt and of Brandt and Raben an attempt was made to assess the value of the zooplankton and of the phytoplankton apart from one another. Seasonal variations have apparently been dealt with only by Wimpenny and Moberg who had the disadvantage of dealing with mixed catches ; but the variation shown in some of the analyses given by Brandt and by Brandt and Raben suggests that seasonal variations in chemical composition take place.

The analyses given by the above authors, with the exception of those by Moberg and Wimpenny, were made on preserved material and no separation of individual species of plants and animals was possible ; in any case, the large numbers they had to deal with would have made such an attempt extremely laborious even if the method of preservation adopted had allowed of it. However, by analysing a number of catches in which certain species of plants or animals predominated, Brandt, and Brandt and Raben, were able to give an approximate figure for the chemical composition of certain groups or species.

The results in the following pages record an attempt to measure the variations in the composition of *Calanus finmarchicus* by itself. *C. finmarchicus* is an important food of certain fish and is widely distributed. In the Clyde Sea-Area it constitutes a considerable percentage of the zooplankton as a whole. The object of the work was to ascertain, in conjunction with the observations on size and distribution by Marshall (1933) and Nicholls (1933) recorded in Parts I and II of this series, what changes in weight and chemical composition took place throughout the year. Although Calanus predominated in all the catches, it was not considered that analyses of the catches as a whole would be of sufficient value and it was decided to separate the Calanus from other species. In addition, since it seemed possible that differences between male, female and the later copepodite stages of Calanus might exist, these were separated before analyses were made. Only living Calanus were used throughout. No stages younger than the fifth copepodite were dealt with largely because of the labour involved in their separation, but also because in actual weight they are relatively unimportant. The collection of material was made by Dr. A. G. Nicholls during the fortnightly visits to Loch Fyne. Very considerable help in the picking out of the Calanus was given by Miss S. M. Marshall and Dr. A. G. Nicholls. All the measurements were made by Miss S. M. Marshall. I have to thank both for making the work possible.

METHODS.

Collection of Material.

Vertical hauls with a 1-metre stramin net were made in the deep water off Strachur in Loch Fyne and the catch suitably diluted and brought to the laboratory. When sufficient numbers could not be obtained by the vertical hauls a horizontal haul was made in deep water. Vertical hauls were preferred since the material was then more likely to be similar to that used for size determination by Marshall (Part II). In the laboratory the Calanus generally lived well and could be kept for several days if the dilution was sufficiently great. If not well diluted the Calanus died off rapidly owing to oxygen depletion and decomposition of the dead ones. In addition, fat globules formed on the surface of the water and this would have vitiated fat analyses. Usually on the day following capture a series of samples of Calanus was taken from the diluted tow-nettings and separated into males, females and Stage V Calanus. Younger stages than this were rejected as it would have required a very large number for analysis and also because their occurrence was less frequent. After some practice the separation can be effected by the naked eye, but in all cases they were finally examined under the microscope. As is shown in the foregoing paper by Nicholls (Part I), the Calanus taken at Strachur consisted generally of a number of stages. At certain times males and females were scarce ; sufficient for analysis could not then be obtained since it involved the examination of very many thousands of individuals. While this is to be regretted, it should be noted that at these times the very fact that they were scarce made them unimportant as a fish food. Stage V was nearly always present in sufficient numbers for analysis and except during breeding periods Calanus in this area seem to live longer in this stage than in any other (Nicholls, Part I).

SIZE AND WEIGHT.

Two samples of about 100 Calanus were measured under the microscope (see Marshall, Part II), each individual in a separate small drop of sea-water on a slide, and transferred alive to a small quantity of filtered sea-water. They were then collected in a sintered glass Gooch crucible, filtered free from sea-water under pressure and given several (generally three) washes with small quantities of distilled water. They were then dried to constant weight at 110° C. Washing with distilled water was necessary to get rid of the adherent sea-water but the washing should not be prolonged or the Calanus may lose some salts or may even lose some fat. Washing was usually completed in two or three minutes. The weight of the dried Calanus was measured to the nearest 0·1 mg. and was generally between 10 and 25 mg. On ignition the weight of ash was less than 1 mg. showing that the washing had been sufficiently good. On the other hand, the weight of ash was too small to be sufficiently accurate for ash determination. Drying at 110° C. was made as short as was consistent with complete removal of water since continued heating at this temperature results in a slight loss of volatile organic material.

Samples used for weight determination could not be used for any other estimations and the weight of these samples was used for determining the protein and fat percentages on separate samples. Transference (after washing with distilled water) of the undried Calanus from a Gooch crucible to a coverslip for subsequent weighing and fat or protein determination was attempted on several occasions but a loss of 1–3 mg. occurred, largely owing to splitting off of fat globules from the Calanus.

ASH.

Ash was determined on a large number of Stage V Calanus on one occasion only, the males and females being insufficient in numbers. The dry weight was obtained as above and the dry Calanus ignited to a white ash at red heat with the Bunsen burner. This procedure is likely to have resulted in a certain amount of loss by volatilisation of sodium and potassium chlorides and the ash percentage given is a minimum value for the time of year at which the estimation was made. A more elaborate procedure was not advisable with the small quantity of material available and in any case the loss is not likely to have been great.

PROTEIN.

Protein was estimated from the total nitrogen content. Duplicate samples of 100 Calanus were combusted with sulphuric acid in the presence of potassium sulphate and a trace of copper and the ammonia formed estimated by Folin's micro-aspiration method (Plimmer, 1920). In the calculation of protein content the customary factor (N × 6·25) has been used. No allowance has been made for the presence of chitin which contains only about 6% N, whereas protein contains about 16% N. Chitin analyses could only be made on large numbers of Calanus (see below) and sufficient numbers could not be obtained regularly. Since Calanus varies in weight considerably in the course of the year, it is unsafe to make a constant correction for chitin nitrogen throughout.

Fat.

Fat was estimated by Stoddard and Drury's saponification method (1929) with some slight modifications. Duplicate samples of 100 Calanus were transferred from the microscope slide to a small basin and there ground up with the alcohol-ether mixture. The whole was then transferred to a 100 c.c. flask with the alcohol-ether mixture. The subsequent treatment was then similar to that described by Stoddard and Drury with the exception that a fat-free filter paper was used instead of the Gooch crucible suggested by them (see Stewart, Gaddie and Dunlop, 1931) and phenolphthalein was used as indicator. The factor used for conversion of titration value to fat was that for triolein. This was used by Brandt and Raben (1919–22) and is within the range given for Calanus in a recent paper by Klem (1932).

Chitin.

A large number (1000) of Stage V Calanus was treated for a short time with dilute hydrochloric acid and then for a considerable time with 15% caustic soda at 100° C. When clean, the residue was collected on a sintered glass Gooch crucible, washed successively with water, alcohol and ether, dried at 110° C. and weighed. The quantity of chitin present was small even in 1000 Calanus and the weight of the ash of the chitin on ignition lay within the experimental error of weighing.

No determinations of carbohydrate were made since a direct estimation would have involved a large number of Calanus and the indirect method of estimation employed by Brandt (1898) and others could not be adopted.

RESULTS.

Size and Weight.

The seasonal variation in the weight of male, female and fifth copepodite Calanus is shown in Figure 1 and Tables I, II and III. As has been mentioned, only Stage V Calanus could be obtained in sufficient numbers regularly and the curves for male and female Calanus are incomplete.

Adult male Calanus were obtained in sufficient numbers for analysis on only four occasions and the dry weight varied from 23·5 mg. to 18 mg. per 100 Calanus. There was a gradual fall in weight from February to May which is related directly to a decrease in size during that time. They were also largest and heaviest during their period of maximum abundance for the year.

Adult female Calanus were obtained fairly regularly from the beginning of March till the end of August. The weight of 100 Calanus varied from 19·5 mg. to about 11 mg. The variation in weight is irregular with a pronounced high peak in May and a fall thereafter. The curve for weight again shows a relation to size especially in the pronounced high peak in May. There is, however, only a slight correspondence between weight and numbers ; the May peak in weight and size is associated with a very small increase in numbers of females.

Stage V Calanus show greater variations in weight than either males or females and they were available over a much longer period. In the winter of 1931 the greatest weight was 28 mg. per 100 Calanus. This was associated with their presence in very large numbers at this time. During the period from January to April the weight of 100 Calanus rapidly fell and the minimum was reached early in May when 100 Stage V Calanus weighed only about 10 mg. which is approximately a third of the winter value. After this the weight increased rapidly and reached the maximum for the autumn of 1932 in August and September at 23·5 mg. per 100 Calanus. There is a certain correspondence between numbers of Stage V Calanus and weight. The spring decrease in weight is coincident with the rapid disappearance of the large winter stock of Stage V Calanus. According to Nicholls (Part I) the first breeding period of Calanus for the year began early in March so that the nadir of the weight curve (May 2nd) came on a date when the Stage V Calanus would be expected to consist of individuals belonging to the end of this breeding period. Sufficient numbers for weight determinations were not obtained between the beginning of March and the beginning of April so that the weights during this period could not be obtained. Even on May 2nd only 60 individuals were available for weighing and some doubt exists as to the true state of affairs during this period. With the arrival of the second brood, weight rose rapidly though it was still well below winter values. The increase in weight continued thereafter, but the values ultimately reached were considerably lower than those of the previous winter. This again appears to correspond with numbers to some extent for the stock of Calanus late in 1932 was much lower than that of the winter of 1931–32. The relation of size to weight for Stage V Calanus is not so marked as with males and females but there is a general correspondence of the curves. As has already been mentioned, the catches used for analysis were not the same as those used by Marshall (Part II) for size determination and, as might be expected, the relation between weight and size in the samples actually weighed is closer than that between weight and size in the samples measured and recorded by Marshall (Part II). This is to be explained partly by the fact that the stramin net used for the capture of specimens for analyses probably exerts a certain selection on fifth copepodite Calanus; in addition the samples used for weight determination were measured alive while those used for size measurement by Marshall (Part II) were preserved in formalin which causes a slight swelling of the Calanus.

Although it has been shown that when taken separately, there is a relation between size and weight in male, female and Stage V Calanus, the curves (Fig. 1) demonstrate clearly that the weight depends chiefly on the kind of Calanus being dealt with (male, female or Stage V) and the time of year. Thus, for example, on August 22nd the average size of 100 female Calanus was 2·34 mm. and the weight 11·3 mg.; on the same date 100 Stage V Calanus had an average size of only 2·24 mm. (0·10 mm. *less* than that of the females) and yet the weight (23·5 mg.) was more than *double* that of the females. This anomalous relationship of size to weight between female and Stage V Calanus held from late May till the end of August and probably continued later in the season when females were scarce. It is probably to be accounted for by differences in water content.

During the period from March to May when Stage V Calanus were very light, both males and females were from 50–100% heavier than they; males were somewhat lighter than Stage V Calanus in May in spite of the fact that they were definitely larger. So far as can be said from the small number of observations available, male Calanus are heavier than female Calanus in spite of the fact that the latter are generally larger.

From the above remarks it is obvious that dry weight determinations on a catch containing males, females and Stage V Calanus without a preliminary separation of these, must lead to results which are of little value. It is also apparent that the food value of Calanus does not depend entirely on the numbers present but is influenced very considerably by the dry weights of the different stages at different times of the year.

It was unfortunate that the collection of samples for analysis was limited to Loch Fyne, for, as is shown by Nicholls (Part I), the catches there showed less numerous fluctuations and the variations in the sizes of the different broods were also small (Marshall, Part II).

Hitherto no direct weighings of dried Calanus have been available but some estimations of the weights of copepods without reference to species have been made by Brandt (1898). According to him one gram of dry material is contained in between 3×10^5 and 7×10^5 copepods with a probability that the range is only from 3×10^5 to 5×10^5. In the observations on Calanus from Loch Fyne, the numbers per gram dry weight were

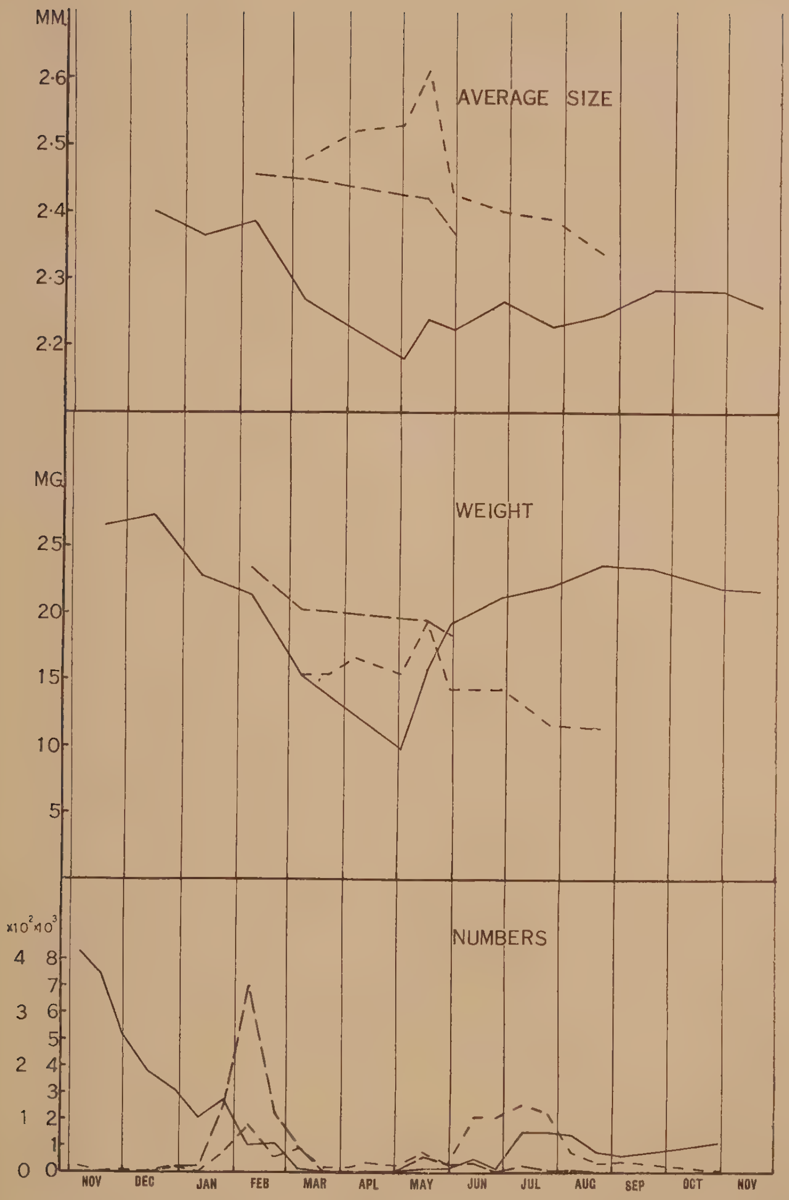

Fig. 1.—Size, weight and numbers of Calanus from Strachur, Loch Fyne.
——— StageV, — — — VI ♂, - - - - - VI ♀.
Average size in mm. of ca. 100 individuals.
Weight in mg. per 100 individuals.
Numbers taken in one vertical haul (Part I) (V, × 10^3, VI ♂ and VI ♀, × 10^2.).

found to be very much smaller; one gram dry material was contained in 3500 Calanus as a minimum and in 10,000 as a maximum. It should be remembered in this connection, however, that *Calanus finmarchicus* is large compared with the average size of the copepods of the southern North Sea and that the earlier copepodite stages of Calanus have not been dealt with in the analyses from Loch Fyne.

Estimations of the wet weight of Calanus from the Barents Sea have recently been made by Bogorov (1933). The method of weighing adopted by this author (fixation in formalin and drying with filter paper) does not allow of a high degree of accuracy, but is useful in comparing the changes in weight through the copepodite stages to adult. His results showed that adult female Calanus were lighter than Stage V Calanus as has also been found in this area. In the Barents Sea, however, the females were *smaller* than the Stage V Calanus indicating that in this case the females which were lighter probably belonged to a different brood. A close comparison of the results is not possible since his observations were based on a single haul and no seasonal observations were made. His results show that to obtain a suitable quantity of material for analyses of the earlier copepodite stages of Calanus several thousand individuals would be required.

The size measurements in the present paper are those of the length of the cephalothorax while Bogorov measured the length from the head to the tips of the caudal furcæ. It has been found (by Miss S. M. Marshall) that this makes Bogorov's measurements some 20% greater than those recorded in this paper. As has already been mentioned, the method of fixation employed by Bogorov (formalin) may cause a slight swelling of the Calanus. Allowing for these corrections, the largest Stage V and female Calanus found in Loch Fyne are only about 90% of the size of those found by Bogorov in the Barents Sea. If we compare the dry weight of the largest Calanus found in Loch Fyne with the wet weight of the Calanus weighed by Bogorov, we find that about 80% consists of water. This, however, is not a reliable figure for the degree of drying used by Bogorov was empirical and the effect of the formalin on weight may also be appreciable.

ASH.

Since the ash percentage is low, a large number of Stage V Calanus (over 1500) were separated from a catch and collected on a sintered glass Gooch crucible. They were washed several times with distilled water as rapidly as possible and then dried to constant weight at 110° C. The dry mass was then gently ignited till free from carbon, cooled and weighed. The ash was white and weighed 12·9 mg. which was 3·6% of the dry weight of the Calanus. No estimations could be made on male or female Calanus as they were relatively scarce. No analyses of the inorganic constituents of the ash were made.

Figures for the percentage of ash in the plankton have already been given by Brandt (1898), Brandt and Raben (1919–22), Moberg (1926) and others. For a haul rich in copepods, Brandt gives a corrected figure of 7·12% and an average for copepods of 9·3%; Brandt and Raben in their tables give values of 4·24 and 6·42% which are fairly close to those obtained by using *Calanus finmarchicus* alone. Moberg, using material from tow-nettings taken 10 miles off La Jolla, obtained a minimum value of 4% but does not state the composition of the catch. The inshore values obtained by Moberg are very high and are no doubt caused by the silt present.

While the value found (3·6%) in Stage V Calanus probably holds for the major part of the winter, it is possible that there will be changes in ash content associated with the changes in weight.

FAT.

Analyses on adult males and females were limited owing to the difficulty in obtaining specimens in sufficient numbers. Stage V, however, were obtained more regularly. The results of the fat determinations on these are shown in Table III and Figures 2 and 3. The fat content follows the weight curve in general with two exceptions. At the beginning of March with Stage V Calanus the fat content was considerably higher than would be expected had it followed the weight curve and this is shown more clearly on the curve for fat percentage. The lowest value for fat coincided with the lowest point on the weight curve but the lowest percentage of fat was a fortnight later. It is not possible to say whether the peak in fat in March is associated with the spring increase in the phytoplankton, but the fact that the fat content was lowest during the summer when diatoms though not abundant are rarely absent does not support this conclusion. The agreement with the weight curve is to be expected though the high average value for fat content in the autumn and winter is puzzling when we consider that at that time plant food is scarce. Further work will be necessary before the relationship if any of the fat content of Calanus to abundance of phytoplankton can be found.

Analyses of female Calanus were not sufficiently numerous to show whether or not the fat content varied with the state of maturity. They do show, however, that contrary to expectation, female Calanus were less rich in fat than either male or Stage V Calanus.

The results recorded in the present paper are considerably higher than those given by Brandt and by Brandt and Raben for mixed plankton catches in the southern North Sea. They are considerably higher than those of Wimpenny who also worked on mixed catches. A possible objection to the method adopted in the present paper is that the assumption is made that the samples of 100 Calanus used for fat determination have the same weight as the samples used for weight determinations. The difference in weight in duplicate samples taken from a single tow-netting is seldom great (Tables I, II and III) and only exceeded 2 mg. on one occasion (8% error) so that this is not the explanation of the difference. The explanation more probably is that in the present work one stage of a single species is dealt with while the above-mentioned authors dealt with mixed catches.

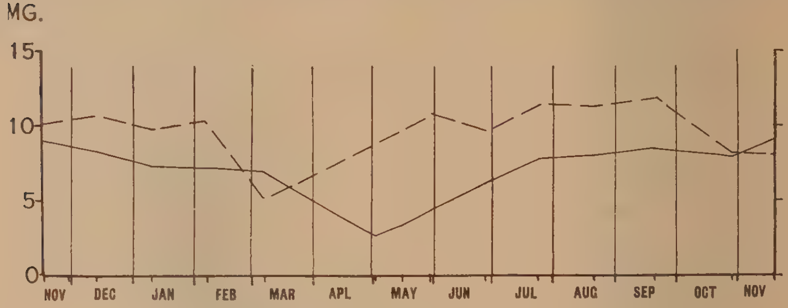

FIG. 2.—Weight of fat and protein per 100 Stage V Calanus.
Fat ————. Protein — — —.

Seasonal observations have been made by Wimpenny (1929) and he records his results as mg. fat per 1000 zooplankton individuals. The maximum fat content in the North Sea was found in August and the minimum in October. Stage V Calanus in the Clyde Sea-Area on the other hand had its maximum fat content in March while the results in spring and autumn were uniformly high. Wimpenny's results, however, are based on the weight of fat per 1000 individuals; since he dealt with mixed catches of varying composition and since as shown in the present

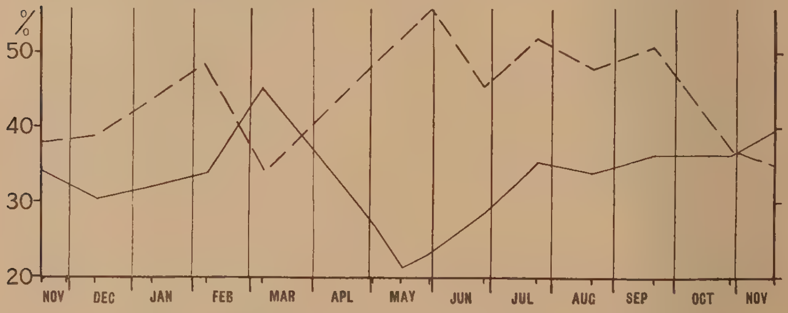

FIG. 3.—Percentage of fat and protein in Stage V Calanus.
Fat ————. Protein — — —.

paper the weight of a given number of individuals may vary considerably in the course of a year, his results should be interpreted with caution.

There is no obvious relation between the percentage of fat in Stage V Calanus and the different broods throughout the year. The first brood of Stage V Calanus had low fat values and thereafter later broods were fatter till the autumn-winter brood with the usual high fat values appeared. Stage V Calanus appears, in the Clyde Sea-Area at any rate, to be the most numerous stage of this important fish food for the major part of the year (Nicholls, Part I) and in view of the results of other authors on mixed plankton catches, it must be classed as one rich in fat.

The results of fat determinations on adult male and female Calanus are not numerous enough for any seasonal changes to be deduced. In adult male Calanus the value fluctuated between 18 and 34% and in adult females between 11 and 30%. Both are less fat on the whole than Stage V Calanus. The low fat values in females were unexpected and the changes recorded showed no relationship to the breeding periods recorded by Nicholls (Part I).

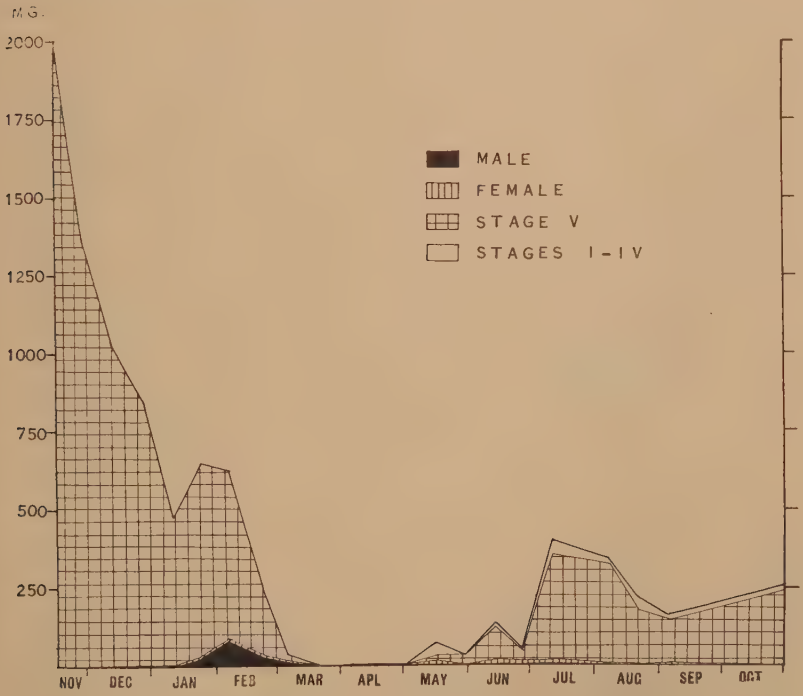

FIG. 4.—Calculated dry weight in mg. of vertical hauls throughout the year showing weight of different sexes and stages.

PROTEIN.

Like fat estimations, nitrogen determinations could only be made on a few occasions with adult male and female Calanus. Even with Stage V Calanus more numerous estimations would have been desirable. The results are shown in Tables I, II and III, and Figures 2 and 3. No reliable estimations could be obtained between February and May when the changes in weight and fat content were most marked. Protein values generally amounted to about 50% of the dry weight of the Stage V Calanus and fluctuated between 35 and 55%. A low value was obtained in the beginning of March on the same date as that on which the fat content was unusually high and in the autumn of 1932 values fell from 50 to 35%. This fall in protein content was not shown in the autumn and winter of 1931–32 when numbers were very much higher.

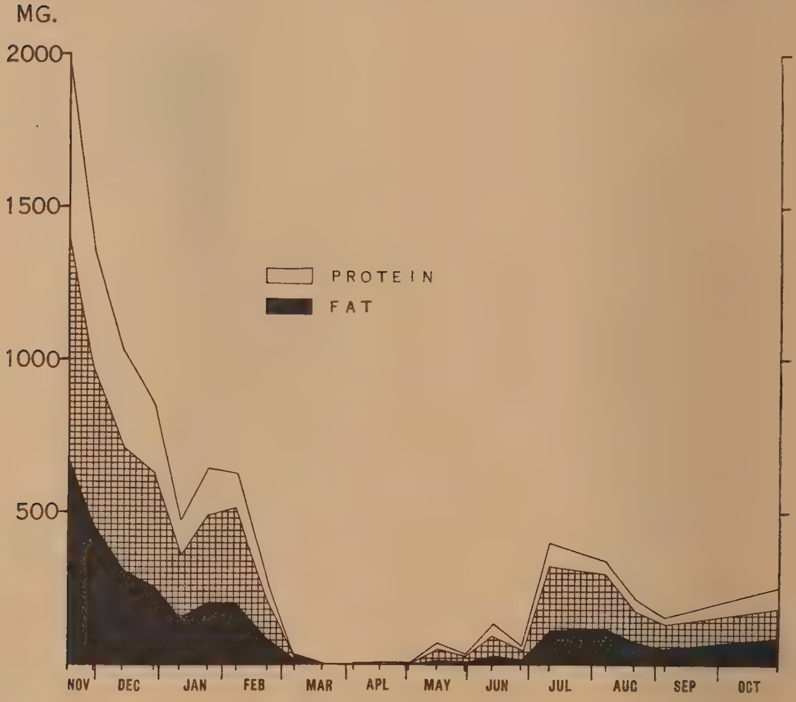

FIG. 5.—Calculated weight of protein and fat per vertical haul.

Adult female Calanus were richer in protein than Stage V Calanus and the level remained high (75%) on all four occasions on which estimations could be made. Adult male Calanus were much the same as Stage V with values varying from 40–70%.

The figures given for protein content of Calanus are considerably lower than those recorded by Brandt and by Brandt and Raben. The explanation of this discrepancy lies apparently in the fact that Calanus is richer in fat than the mixed plankton catches analysed by these authors. No seasonal observations have hitherto been recorded in protein content of plankton.

In the figures given above and in Tables I, II and III no correction is made for the nitrogen present in the chitinous parts of the Calanus.

CHITIN.

An analysis of the chitin was made on only one occasion and on Stage V Calanus alone since it was necessary to use at least 1000 individuals. The Stage V Calanus used for the determination were from the winter stock and the chitin content is probably fairly constant then since they do not moult till early in the year. The amount of chitin in 1000 Stage V Calanus was 6·1 mg., equivalent to 2·98% of the dry weight of the Calanus. This is somewhat lower than the figures given by Brandt and Raben (1919–22) which are 4·37% and 5·02%.

The object of the chitin determination was to find out what fraction of the organic material could definitely be classed as indigestible. Only a comparatively small number of animals is able to digest chitin and with most animals it appears to be excreted unchanged.

THE FOOD VALUE OF CALANUS IN LOCH FYNE IN 1932.

In Figures 4 and 5 and Table IV is shown the calculated total dry weight of the Calanus in the tow-nettings made by Nicholls (Part I) at Strachur in Loch Fyne. Figure 4 shows the weight composition of the catch as male, female, Stage V and Stages I–IV Calanus. The weights have been calculated from the dry weight determinations on 100 individuals except for Stages I–IV when the calculations have been based on Bogorov's (1933) figures making allowance for the water content. According to his figures,

1 Stage V Calanus equals in dry weight about 1·8 Stage IV.
1 ,, V ,, ,, ,, ,, ,, 11 Stage III.
1 ,, V ,, ,, ,, ,, ,, 42 Stage II.
I ,, V ,, ,, ,, ,, ,, 60 Stage I.

The weight figures for Stages I–IV are probably not very accurate but the diagram (Fig. 4) shows that they are relatively unimportant. The nauplius stages of Calanus and the eggs must weigh very much less individually and even the very high numbers met with at times (Nicholls, Part I) will have but little effect on the total weight curve.

Stage V Calanus is responsible for the bulk of the weight except for a short period from the middle of March to the end of April when the total weight of the catch was also very low ; males and females were of importance only spasmodically. During the autumn and winter practically the whole weight of the catch was due to Stage V Calanus. In the winter of 1931 they were very much more numerous and also somewhat heavier than in the winter of 1932 which suggests that there may be considerable fluctuations from year to year.

In Figure 5 and Table IV are shown the weights of fat and protein in the catch throughout the year. The curves for these run fairly parallel to the total weight curve. The fraction unaccounted for will consist partly of ash and chitin and probably to a large extent of carbohydrate (Brandt, 1898). The net used filtered an area of 0·196 sq.m. so that the figures represent the weight of Calanus and of protein and fat below each 0·196 sq.m. of surface. The average depth at Strachur was 130 m. so that the material was distributed through 25·5 cubic metres of water.

SUMMARY.

1. The dry weight of 100 male, female and Stage V Calanus in Loch Fyne fluctuated throughout the year. 100 Stage V Calanus in May weighed only about $\frac{1}{3}$ of what they did in December. Male and female Calanus also fluctuated considerably in weight.

2. Stage V Calanus is usually largest and heaviest when it is most abundant. With male and female Calanus size and weight are related.

3. Stage V Calanus, in spite of being smaller than female Calanus, was from the beginning of June till the end of August considerably heavier (over 100%). When Stage V Calanus was at its lightest and smallest, it weighed less than female Calanus at the same time.

4. The weight of Stage V Calanus fell during the spring and did not increase again till after the end of the first breeding period.

5. The fat and protein content of Calanus depends chiefly on dry weight. The values obtained for fat content were considerably higher than those hitherto recorded for zooplankton and those of protein lower.

6. The ash content is about 3·6% and the chitin content about 3% of the dry weight.

7. Stage V Calanus accounted for by far the most important part of the total weight of the catch throughout the year.

8. The total food value of the Calanus in Loch Fyne probably varies very considerably from year to year.

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TABLE I

Weight and Composition of Male Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
8.2.32 . .	22·5	2·45	21·9	56
	24·0	2·46	–	53
7.3.32 . .	20·2	2·45	33·7	–
	20·3	2·45	31·7	–
	20·1	2·45		
16.5.32 . .	19·4	2·42	19·6	69
			18·0	–
30.5.32 . .	18·8	2·36	22·9	59
	17·8	2·37	23·5	54

TABLE II.

Weight and Composition of Female Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
7.3.32 . .	15·2	2·48	29·6	–
		2·48	24·3	–
21.3.32 . .	15·2	2·51	16·3	–
	15·5	2·49	16·3	–
5.4.32 . .	17·7	2·54	11·4	74
	15·5	2·51	12·6	73
2.5.32 . .	15·4	2·53	21·4	–
16.5.32 . .	19·4	2·61	12·4	–
			12·9	–
30.5.32 . .	14·6	2·41	21·1	77
	13·9	2·44	17·6	74
27.6.32 . .	14·2	2·40	13·3	79
	14·3	2·40	10·5	69
25.7.32 . .	11·7	2·39	15·6	77
	11·3	2·39	–	–

TABLE III

WEIGHT AND COMPOSITION OF STAGE V CALANUS.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
17.11.31	25·4 27·5	– –	34·4 33·6	32 44
14.12.31.	26·6 28·0	2·40 2·40	28·9 31·5	42 36
11.1.32	22·9 22·5	2·36 2·37	31·2 33·0	44 44
8.2.32	21·0 21·5	2·39 2·38	34·4 33·4	48 49
7.3.32	15·2	2·27	46·6 44·1	34 –
2.5.32	9·7	2·18	26·8	–
16.5.32	15·7 15·2	2·22 2·25	22·7 20·1	– –
30.5.32	19·1 –	2·20 2·25	23·1 –	56 –
27.6.32	21·7 20·4	2·27 2·26	26·1 31·3	46 45
25.7.32	22·2 21·7	2·24 2·22	35·5 –	52 –
22.8.32	23·4 23·6	2·25 2·24	34·9 32·8	46 50
21.9.32	23·6 23·0	2·28 2·29	33·9 38·6	51 –
30.10.32	21·6 21·9	2·26 2·30	36·8 35·8	30 44
21.11.32	22·1 23·1 20·4	2·24 2·28	39·8 –	35 35

TABLE IV.

Weight and Composition of Vertical Hauls taken in Loch Fyne.

Date.	No of individuals per vertical haul.	Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
17.11.31	V. 7420	1962·6	747·6	668·5
	IV. 30	4·4		
		1967		
30.11.31	♀ 5	0·8	0·6	0·2
	V. 5120	1354·2	515·4	461·2
	IV. 15	2·3		
		1357·3	516·0	461·4
14.12.31	V. 3750	1023·8	401·5	310·3
	IV. 30	4·5		
		1028·3		
29.12.31	♂ 10	2·3	1·3	0·5
	♀ 10	1·5	1·1	0·4
	V. 3087	842·8	369·2	254·8
	IV. 7	1·0		
		847·6	371·6	255·7
11.1.32	♂ 10	2·3	1·3	0·5
	♀ 4	0·6	0·4	0·2
	V. 2070	469·9	205·7	150·8
	IV. 2	0·3		
		473·1	207·4	151·5
25.1.32	♂ 128	29·8	16·2	6·5
	♀ 37	5·6	4·1	1·5
	V. 2685	609·4	267·1	195·9
	IV. 8	1·0		
		645·8	287·4	203·9
8.2.32	♂ 348	80·9	44·1	17·7
	♀ 58	8·8	6·5	2·4
	V. 2515	534·4	261·9	181·4
	IV. 10	1·2		
		625·3	312·5	201·5
23.2.32	♂ 113	26·3	14·3	5·8
	♀ 28	4·6	3·4	1·2
	V. 1056	224·4	109·8	76·1
	IV. 2	0·2		
		255·5	127·5	83·1

Date.	No. of individuals per vertical haul.		Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
7.3.32	♂	48	9·7	5·2	3·2
	♀	46	7·0	5·1	1·9
	V.	142	21·6	7·4	9·8
	I.	1	0·0		
			38·3	17·7	14·9
21.3.32	♂	6	1·2	0·7	0·4
	♀	8	1·2	0·9	0·2
	V.	7	1·1	0·4	0·5
	IV.	1	0·1		
			3·6	2·0	1·1
5.4.32	♂	3	0·6	0·3	0·2
	♀	8	1·3	0·9	0·2
	V.	8	1·2	0·4	0·6
	IV.	1	0·1		
	II.	1	0·0		
	I.	10	0·0		
			3·2	1·6	1·0
18.4.32	♂	3	0·6	·3	0·2
	♀	17	2·8	2·1	0·3
	V.	22	3·3	1·4	1·9
	IV.	10	0·8		
	III.	2	0·0		
	II.	3	0·0		
			7·5	3·8	2·4
2.5.32	♂	2	0·4	0·3	0·1
	♀	13	2·0	1·4	0·4
	V.	21	2·0	2·3	1·1
	IV.	38	2·0		
	III.	5	0·0		
	II.	1	0·0		
	I.	6	0·0		
			6·4	4·0	1·6
16.5.32	♂	28	5·4	3·7	1·0
	♀	38	7·4	5·4	0·9
	V.	122	18·8	32·3	12·3
	IV.	314	26·8		
	III.	796	10·9		
	II.	187	0·7		
	I.	56	0·1		
			70·1	41·4	14·2
30.5.32	♂	13	2·4	1·4	0·6
	♀	16	2·3	1·7	0·4
	V.	132	25·2	17·1	7·0
	IV.	39	4·1		
	III.	44	0·7		
	II.	53	0·2		
	I.	22	0·1		
			35·0	20·2	8·0

Date.		No. of individuals per vertical haul.	Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
13.6.32 . .	♂	17	3·1	1·8	0·7
	♀	102	14·5	10·9	2·8
	V.	501	105·4	53·1	26·7
	IV.	80	9·3		
	III.	30	0·6		
	II.	40	0·2		
	I.	70	0·2		
			133·3	65·8	30·2
27.6.32 . .	♂	3	0·5	0·3	0·1
	♀	102	14·5	10·9	1·7
	V.	177	37·3	20·2	12·6
	IV.	36	4·2		
	III.	93	1·7		
	II.	93	0·5		
	I.	60	0·2		
			58·9	31·4	14·4
11.7.32 . .	♂	13	2·4	1·4	0·6
	♀	127	18·1	13·4	2·2
	V.	1537	337·4	196·7	108·8
	IV.	326	39·5		
	III.	104	2·0		
	II.	21	0·1		
	I.	13	0·0		
			399·5	211·5	111·6
8.8.32 . .	♂	3	0·5	0·3	0·1
	♀	36	4·1	3·1	0·6
	V.	1442	316·5	174·3	119·2
	IV.	160	19·3		
	II.	1	0·0		
			340·4	177·7	119·9
22.8.32 . .	♂	2	0·4	0·2	0·1
	♀	16	1·8	1·3	0·3
	V.	743	174·6	103·0	72·7
	IV.	311	40·4		
	III.	2	0·0		
			217·2	104·5	73·1
5.9.32 . .	♂	2	0·4	0·2	0·1
	♀	19	2·1	1·6	0·3
	V.	609	141·9	78·8	52·0
	IV.	90	11·6		
	III.	2	0·1		
	II.	4	0·0		
			156·1	80·6	52·4
30.10.32 . .	♂	1	0·2	0·1	0·0
	♀	5	0·5	0·4	0·1
	V.	1110	241·4	93·6	91·9
	IV.	96	11·5		
			253·6	94·1	92·0

Development of *Scolecolepis fuliginosa* (Claparède).

By

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With 16 Figures in Text.

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INTRODUCTION.

MUCH is already known of Spionid larvæ from descriptions of planktonic forms, but very few species have been reared from the egg through the larval stages to metamorphosis. The egg and early stages of Scolecolepis are figured by McIntosh (1915) and by Claparède and Micznikow (1868), but there is no complete account of the development to be found in the literature. By the courtesy of the Director of the Marine Laboratory at Plymouth I was able to undertake this work, and I am indebted both to Dr. Allen and Mr. D. P. Wilson for advice and help during the course of the research.

In the arrangement of the paper the aim has been to describe fully certain stages in the life history, and to give as concise an account as possible of the development from one stage to the next.

METHODS.

Scolecolepis fuliginosa (Claparède) lives in black mud containing a large percentage of decomposing organic matter, and though localised, the worms are plentiful. At Plymouth they were obtained near the high-tide mark at Rum Bay, where they are covered by the tide for only two to three hours out of the twelve. The oxygen content of this mud is probably low. The worms live in sandy tubes lined with mucus, and the specimens were obtained by lifting loose stones and examining the mud beneath.

The mature worms were carried to the laboratory with the mud in which they live, and there allowed to clean themselves in sea-water. As it is impossible to ascertain the sex without injury to the worm, the whole sample was placed in a finger-bowl, where eggs and sperm were slowly extruded. Half an hour later, the eggs were removed with a pipette, washed free from sperm and placed in a sterilised finger-bowl with filtered sea-water. As soon as the young larvæ had begun to swim, the unfertilised eggs were removed and a few drops of Nitzschia culture, kindly supplied by Dr. Allen, were added as food. When the larvæ were found to be healthy, most of them were transferred to a plunger-jar, the remaining few being retained for continuous observation in the finger-bowl. These latter did not grow as quickly as those in the plunger-jar. From time to time, larvæ were removed and trapped on a cavity slide for observation, care being taken that they were not distorted by pressure; others were killed at various ages by squirting hot Bouin on to them when swimming in a watch-glass. Bouin between 60° and 70° C. was found most suitable. Before sectioning they were first orientated on a piece of stained Ulva, to which they were attached by a solution of collodion in clove oil, which is hardened in equal parts of xylol and chloroform. This is a modification of the process recommended by N. Yatsu (1903). In general, the methods employed were those of Mr. D. P. Wilson.

Larval Development.

The unfertilised egg (Fig. 1) is very similar to that figured by Cunningham and Ramage (1888), Pl. XXXVI for Nerine. It is ellipsoidal, averaging 160μ long and 100μ broad, but size and shape are both variable. The cytoplasm is brown both by transmitted and reflected light. The margin of the egg is lobulated and there is a pale germinal vesicle near the centre, the whole being enclosed by an egg-membrane which appears to be very thick on account of its curious folds, which give the surface the appearance of a honeycomb. This membrane is punctate both internally and externally, the depressions on the one side corresponding to the elevations on the other.

About two hours after fertilisation the germinal vesicle and the lobulated margin are lost, and the cytoplasm rounds off within an inner fertilisation membrane (Fig. 2). Between the rigid egg-membrane and the contracted mass of cytoplasm a space is left and in this cavity several transparent spherical vesicles are to be seen; these originate on the inner surface of the egg-membrane. Their function is not apparent and they are soon lost in the succeeding cleavage stages. The first cleavage is horizontal, the two cells so formed being unequal in size. Later a four-cell, an eight-cell, and between nine and ten hours after fertilisation a sixteen-cell stage is reached, with four large yolk-laden macromeres and smaller and paler micromeres (Fig. 3). Gastrulation follows by epiboly.

Thus far the egg-membrane remains unchanged, but as the developing mass of cells increases in volume, the membrane is pushed out before it.

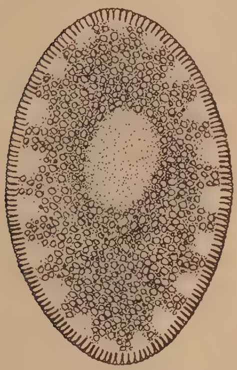

Fig. 1—Unfertilised egg. × 320. Actual length 160μ.

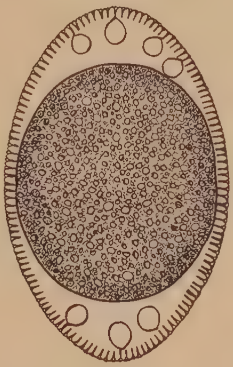

Fig. 2.—Fertilised egg. × 320. Actual length 160μ.

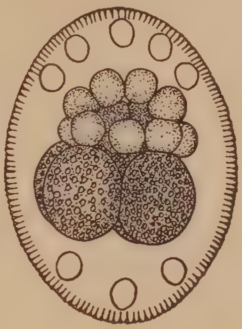

Fig. 3.—Sixteen-cell stage. × 320. Actual length 142μ.

This change in shape is not due to actual stretching of the egg-membrane, but rather to flattening and broadening of the papillæ on its surface. In cases of abnormal development, one part of the egg-membrane may be completely flattened so that a bubble appears on the surface of the larva.

The Trochophore.

The first trochophore (Fig. 4) becomes active and begins to swim less than twenty-four hours after fertilisation. It is about 200μ long, roughly coffin-shaped and dorsoventrally flattened. The colour is brown with a darker area where the gut is foreshadowed by the presence of yolk granules. There is a transparent space between the rigid egg-membrane and the developing mass of cells.

The prototroch is not a continuous line but as in Nerine, it is broken into groups of cilia. In this species there are fourteen groups well separated by longitudinal ridges of protoplasm and the containing egg-membrane. There are eight dorsal groups divided by a very broad median dorsal ridge into two groups of four. On the ventral surface there are six groups, three on either side of the mid-ventral line. The cilia of each group come through a single elongated slit in the egg-membrane.

A group of five very fine cilia form the apical tuft. It is probable that each of these cilia comes through a separate hole in the egg-membrane, for in later stages the apical cilia become separated. There is a single pair of eyes set wide apart on the dorsal surface, at first red but later black. The mouth and anus are formed later.

Development of the Trochophore.

As the larva grows the wrinkled membrane is slowly flattened out, the papillæ becoming broader, the depressions shallower and the whole more closely approximated to the ectoderm.

The head becomes flattened anteriorly, the prototroch ridge forming prominences on either side. A second pair of eyes and then a third are formed on the dorsal surface between the first two, which take up a lateral position anterior to the prototroch. Like the first pair, the second and third are at first red but soon change to black.

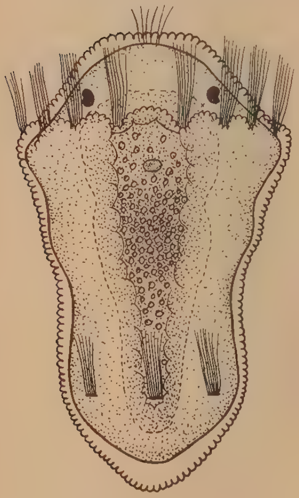

Fig. 4.—Ventral view of the trochophore, 36 hours old. × 320. Actual length 200μ.

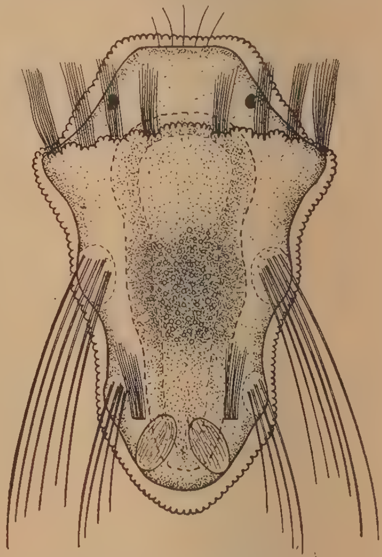

Fig. 5.—Dorsal view of the trochophore, 48 hours old. × 320. Actual length 206μ.

A rounded depression on the ventral surface foreshadows the position of the mouth. The egg-membrane dissolves at this point and the larva begins to feed. The circular mouth soon elongates and appears T-shaped with two anterior grooves. Meanwhile the outline of the gut becomes distinct and the dark yolk-granules are restricted to a rectangular area in the middle of the larva which lengthens and develops into the pigmented stomach-intestine or mid-gut. The anus is formed soon after the mouth.

Thirty-six hours after fertilisation the telotroch is formed, and like the prototroch is not continuous but appears as five separate groups. Two of these groups are dorsal and three are ventral. As the prototroch and telotroch develop, however, each cilia group broadens and the ridges between them disappear, so that the final result is a continuous line of cilia. The dorsal groups of the prototoch move round, and all except one on each side increase in size to form the swimming cilia of the prototroch. The ventral six groups remain small and are soon indistinguishable from the oral cilia which are formed on the sides of the mouth and extend to the ventral surface of the first setiger. The telotroch cilia increase equally in size, forming a continuous line ventrally and laterally, but leaving the broad dorsal gap that is characteristic of Spionid larvæ.

The provisional or larval bristles can first be seen as two minute structures within the prominences behind the prototroch ridges. At an age of two days the first bristle bundles are well developed, each with about four bristles, the largest is 150μ long, and reaches to the end of the larva (Fig. 5). All bristles are slightly curved and beset with spinules on the anterior margin (Fig. 14*a*). A second group and later a third are formed in the lateral elevations which become the parapodia of the second and third setigers. The larval bristles in these and succeding setigers are always slightly shorter than those of the first setiger.

At the time when the bristles of the third setiger become visible, a single pair and later numerous glandular cells are formed below the anus. They are large pale cells probably filled with mucus. Their openings to the exterior are on papillæ on the ventral and lateral surfaces of the anal segment. The function of these mucus cells is not apparent.

The Three-Setiger Larva.

When the larva is three days old the first three bristle bundles are fully formed. The larva is some 250μ long and having lost its coffin-like shape it has become more evenly cylindrical (Fig. 6). The egg-membrane is completely flattened and fused with the ectoderm, forming a persistent cuticle. The colour of the larva is pale brown with a darker area which extends from the beginning of the second setiger to the end of the third indicating the position of the mid-gut.

The head is square in front, a shoulder on each side bearing the swimming cilia of the prototroch. The three pairs of eyes are fully developed, two pairs being dorsal and a larger pair lateral. All three pairs lie on a transverse line across the head, anterior to the prototroch ridge.

There are five well-separated apical cilia. The swimming cilia of the prototroch are very large and like the telotroch cilia, are curled against the sides of the head when not in use. A single prototroch group on the dorso-lateral surface of the head remains small, while ventral groups form the anterior margin of the oral cilia, which now cover the lips and most of the ventral surface of the head (Fig. 6). The oral cilia taper into a neurotroch which extends on to the second setiger. The cilia of the median ventral group of the prototroch have become longer and with the enlarged oral cilia of this region, form an efficient feeding organ. As shown by Wilson (1928) in the development of Polydora, large cilia appear which move independently of the others and probably have a sensory function. They are not as well developed in Scolecolepis as in Polydora, but even at this stage three paired groups are visible, one on the anterior margin of what will become the prostomium, the second in line with the ventral part of the prototroch and the third on the lateral margin of the oral cilia. As has been shown, the oral cilia are continued posteriorly as a neurotroch ; this line of cilia ends on the ventral surface of the second setiger in a depression or "pit," on the margins of which are two or three large sensory cilia. The exact structure of this organ is described in the chapter on the fourteen-setiger larva (see Fig. 15). Paired groups of cilia later appear on the ventral surfaces of the first and second setigers.

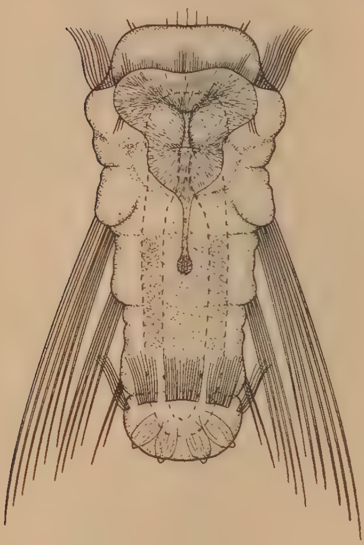

Fig. 6.—Ventral view of the three-setiger larva 4½ days old. × 250. Actual length 250μ.

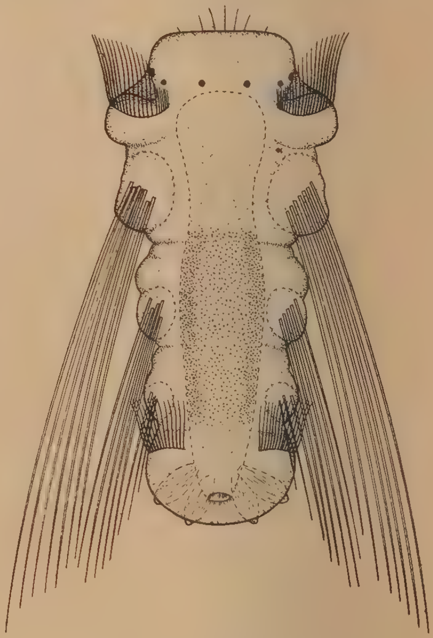

Fig. 7.—Dorsal view of the three-setiger larva, 7 days old. × 250. Actual length 280μ.

The mouth opens into a ciliated vestibule, on either side of which are projecting lips. These lateral lips are separated from a third anterior lip by oblique grooves running from the anterior end of the slit-like mouth. When not feeding a fourth lip projects over the posterior portion of the mouth. But when actively swimming, the mouth is held open, and the shape of the lips is difficult to discern. The narrow gullet is followed by the stomach-intestine, which is characterised by the dark pigment cells that line it. This pigmented portion extends from the second to the end of the third setiger. The last portion of the intestine, the rectum, is pale, and the anus is ciliated.

The segments of the body are marked by projecting seta-sacs (Fig. 7). There are 8 or more larval setæ in the first bristle bundle, the longest of which is 200μ and extends considerably beyond the end of the body. In the second setiger there are 6 and in the third 4, but these numbers are soon augmented.

In the pygidium, the anal glands have increased to 4, each with a distinct papilla on the surface.

Development. With the attainment of the third setiger, growth is apparently less rapid. Though the larva continues to feed, it is not until the 9th day that the fourth setiger is formed. Meanwhile the structures already present increase in size, and the cilia groups develop greatly. The sides of the mouth become slightly pigmented, and the lips more prominent. The larval setæ increase in number as well as length. Finally with the advent of the bristles of the fourth setiger, paired groups of cilia appear on the third setiger which develop into a gastrotroch.

The Four-Setiger Larva.

The larva (Fig. 8) is about 400μ long, with a breadth of 160μ at the first seta-sac. The segments of the body are well marked off by constrictions, and a characteristic mark now forms on that part of the third setiger which becomes the ventral ramus of the parapodium. Pigment is also seen in the dark stomach-intestine, and pale variable marks sometimes appear on each side within the prototroch ridge, as well as a band of brown pigment on the anal segment.

The head is relatively smaller, being no broader than the other segments. The lateral pair of eyes are slightly larger than the others. The prominences of the lateral lips is accentuated, but their general shape remains the same.

The swimming cilia of the prototroch measure 60μ and the cilia of the telotroch 40μ. A single dorsal group of the prototroch remains small (Fig. 9), while the ventral groups have long since merged with the oral cilia. The cilia of the anterior lip and those in the oblique grooves as well as those on the sides of the mouth have enlarged or fused to form broad, plate-like structures which sweep food-particles into the mouth. There are four paired groups of tactile cilia, the newly developed pair being on the posterior edge of the oral cilia. The neurotroch has become broader, the pit deeper, and the sensory cilia which surround it more numerous. There are paired gastrotroch groups on the first three setigers, two small groups on the first, one lateral and one ventral, a single pair on the second and two paired groups on the third.

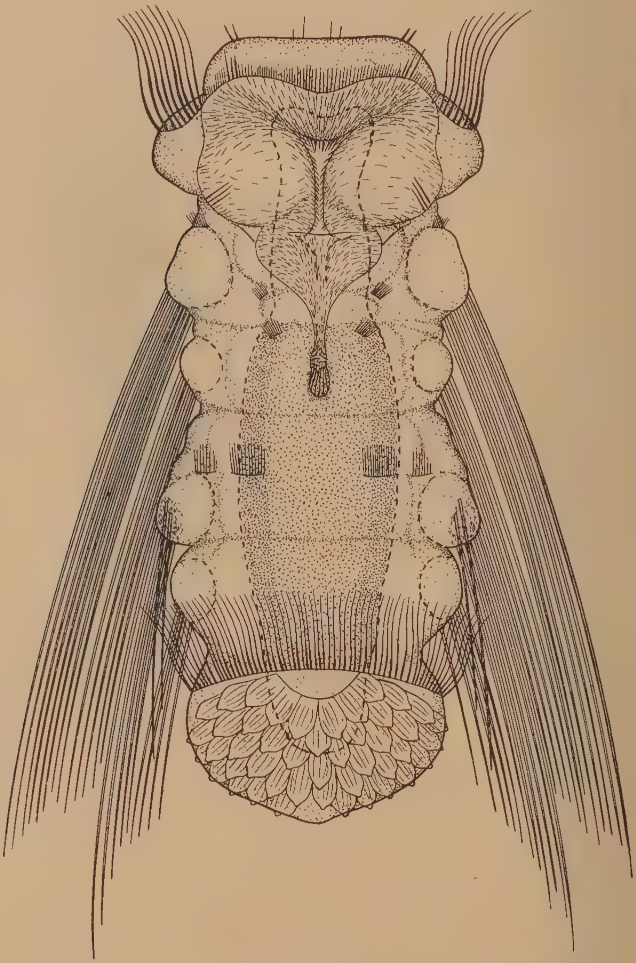

Fig. 8.—Ventral view of a four-setiger larva, aged 9 days. × 270. Actual length 412μ.

The mouth has not changed in shape but the granular pigment has increased on the inner surfaces of the lips ; the stomach-intestine is quite black, and anus is now dorsal in position.

The parapodial prominences show slight division into neuropodia and notopodia. The neuropodial part of the third setiger is slightly pigmented. The number of setæ in the four setigers is respectively 10, 8, 6, 4.

Glands in the anal segment are numerous.

Development. From now on the head remains unaltered, except that in late larval development palpi appear. There is also one more group of tactile cilia formed anterior to the pit on either side of the neurotroch. New segments are added in front of the pygidium, and gastrotroch groups appear on the fifth and later the seventh and ninth setigers, which, with those on the third become important swimming organs. Nototrochs are seen at the six-setiger stage, first on the third setiger and later on the succeeding setigers as well as on the second. In each case six groups unite to form a line across the dorsum. Finally there is the development of the ventral group of larval setæ and the elaboration of the parapodia. The pigment in the ventral ramus of the third setiger is repeated in succeeding setigers, but is not so striking.

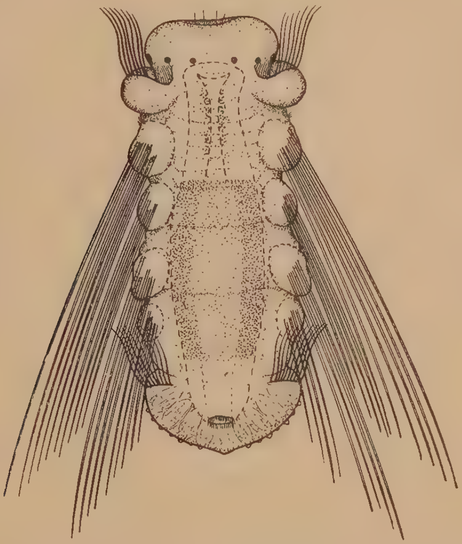

FIG. 9.—Dorsal view of a four-setiger larva, aged 9 days. × 150. Actual length 412μ.

From the four-setiger stage onward it is noticeable that the centre of growth seems to be the third setiger. It is as though growth had previously centred in the head segment and at this stage had shifted back to the third setiger. Later important segmental structures arise first on the third setiger. For example, the differentiation of the parapodia is more advanced in this segment than in preceding or succeeding segments. The ventral groups of larval bristles, the nototrochs and the first group of adult bristles are first seen in this segment. As will be shown this pre-eminence of the third setiger is also evident during metamorphosis.

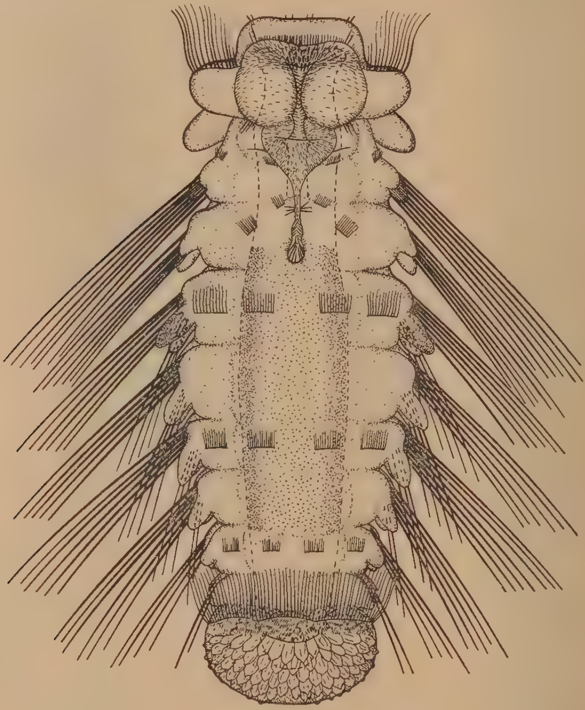

Fig. 10.—Ventral view of an eight-setiger larva, aged 20 days. × 125. Actual length 776μ.

The Eight-Setiger Larva.

The larva at an age of 18 days to three weeks is about 776μ long and has 7–9 setigers (Fig. 10). Larvæ collected from the plankton in Plymouth Sound at this time showed the same development. The body has grown considerably larger with the addition of the new segments. All the structures connected with the larval state are present, and further growth consists in the elaboration of these structures and the addition of new segments.

The body is fairly broad, the parapodia well developed and the head slightly narrower than the rest of the body, except at the prototroch ridge. The only important new pigment marks are pairs of dense black spots on the dorsal surface of the third, fourth, fifth and sixth setigers (Fig. 11). These appear white in reflected light. There is granular pigment on the dorsal surfaces of the succeeding segments, but as these marks are variable they are unimportant for diagnosis. The pigment in the ventral ramus of the third parapodium is now a prominent distinguishing character.

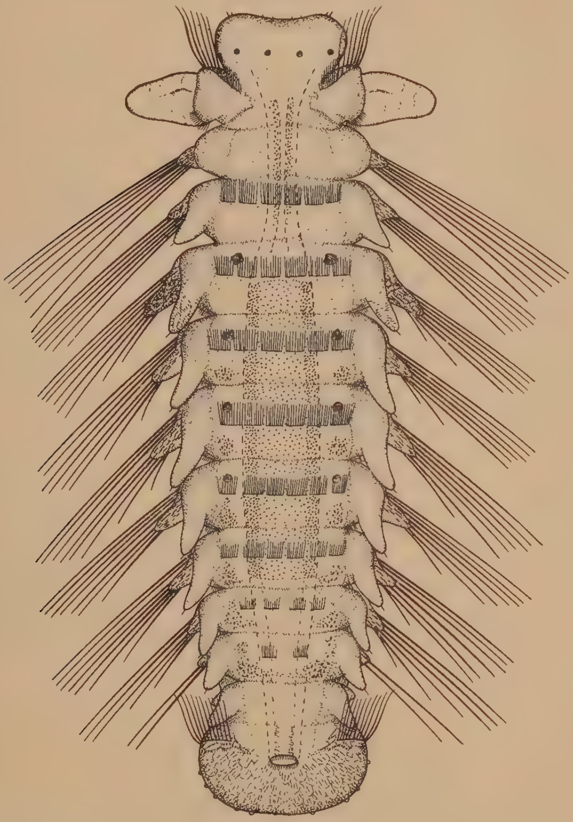

Fig. 11.—Dorsal view of a ten-setiger larva, aged 24 days. × 125. Actual length 0·874 mm.

The head shows little advance, except for the palpi, which appear on the prototroch ridges posterior to the swimming cilia (Fig. 10) and quickly develop into broad stumpy organs, ciliated on both the anterior and posterior margins (Fig. 11). Though called palpi by Fauvel and Ehlers, they are identical with the tentacles described by McIntosh and others. In Wilson's paper on the development of Polydora (Wilson, 1928) they are called tentacles.

The prototroch and telotroch show no advance. The cilia associated with the head have grown longer but no new structures have been formed. In later stages a well-defined row of cilia becomes evident at the base of each palp (Fig. 11) where it arises from the prototroch ridge; scattered cilia cover the surfaces of these organs. The neurotroch with the associated pit cilia and the gastrotrochs on the first and second setigers show no advance. There is an extra group of tactile cilia on either side of the neurotroch near the pit. The gastrotrochs on the third, fifth and seventh setigers grow very large and extend transversely across the ventral surfaces of these segments. Nototrochs have been developed on the dorsal surfaces of all segments from the second to the sixth setiger. These structures never grow large, and though possibly of use in swimming, this is not their main function. They are not lost at metamorphosis and are probably precociously developed adult structures, in which stage they have an important function as will be shown later.

The shape of the mouth has not altered, but the gullet is more strongly pigmented. In each segment the parapodia are prominent, the notopodia and neuropodia well marked, and each notopodium is divided into a branchial and a setigerous region. The larval setæ have reached their maximum development. These number 12 to 14 in the first setiger and have a maximum length of 285μ. In the succeeding segments there are fewer setæ of a smaller size. Thus the third setiger has 8 with a maximum length of 250μ. The adult setæ now appear, but are extremely difficult to distinguish. They are first formed in the dorsal bundle of the third setiger, where a few, short, smooth and more definitely tapered structures indicate their presence.

Development proceeds steadily till metamorphosis, by the addition of new segments in front of the pygidium. About the time that the palpi appear, small groups of cilia arise on the dorsal surface between the parapodia (Fig. 11). These have been called "intersegmental cilia," and are probably homologous with similarly placed, though larger cilia in Polydora, which Wilson (1928) has named "grasping cilia," from their function of holding the larval bristles in place during swimming. These groups, like the nototrochs are precociously developed adult structures which remain small in the larval state. A little later hooded acicular bristles are developed in the neuropodial bundle of the eighth and succeeding setigers. Another pair of gastrotroch groups is formed on the ninth setiger. On the dorsal surface of the pygidium two pairs of small anal cirri are developed.

A résumé of the larva with fourteen setigers and ready to metamorphose is given at this stage.

The Fourteen-Setiger Larva.

At an age of 34–36 days most of the larvæ are about 1·0 mm. long and have fourteen setigers. The body (Fig. 12) is slightly flattened dorso-ventrally, and somewhat broader at the third setiger than elsewhere. The colour is a general pale brown, with scattered chromatophores on

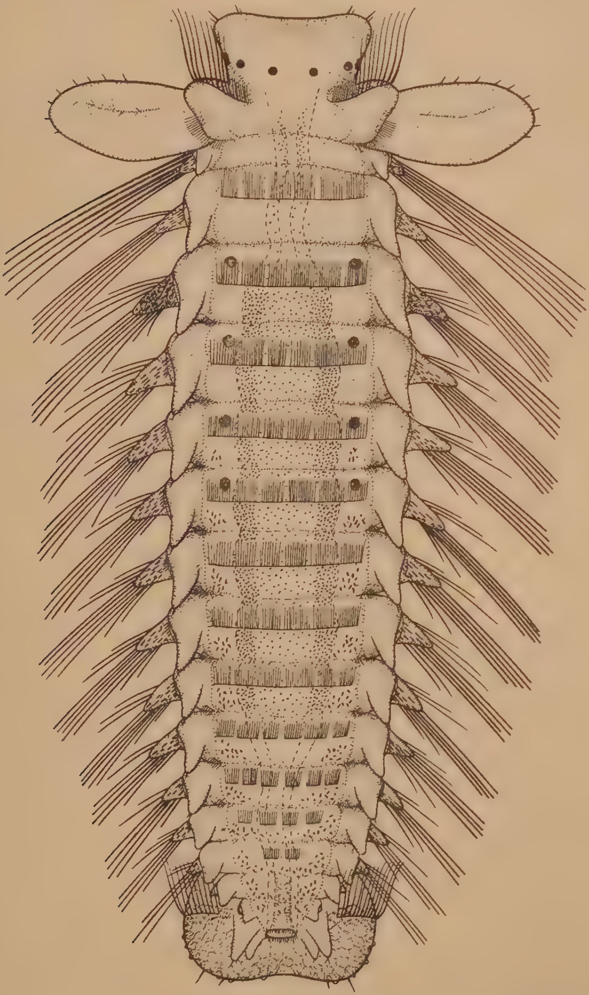

Fig. 12.—Dorsal view of a fourteen-setiger larva, aged 34 days. × 152. Actual length 1·062 mm.

the posterior segments. The neuropodium of the third setiger is dark brown and the third, fourth, fifth and sixth setigers have dense pigment spots. There is granular pigment in the œsophagus and the stomach-intestine is black. That part of the pygidium which bears the telotroch is brown and the posterior, glandular part is bluish.

The prostomium is square in front with a slight median depression. The three pairs of eyes form an inverted crescent across the dorsal surface, the outer pair being almost hidden by the prototroch ridge, which forms the base of the palpi. From now on this part of the head will be called the palpophore. The palpi themselves are broad and flattened.

The swimming cilia of the prototroch are now 68μ long and the telotroch cilia 55μ. The other cilia structures associated with the head and the neurotroch are unchanged. The gastrotroch groups on the anterior segments remain small, but those on the third, fifth, seventh and ninth setigers are large swimming organs. Although Wilson has found that the position of the gastrotrochs is variable in Polydora, in Scolecolepis they seem constant. All setigers from the second onwards bear nototrochs and intersegmental cilia.

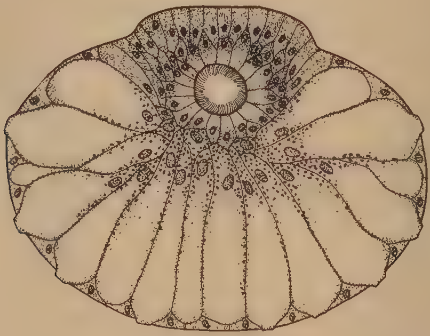

Fig. 13.—Transverse section through the anal segment of a fourteen-setiger larva. × 400.

The structure of the pit is shown in Figure 15, which represents a longitudinal section through a slightly contracted larva. As the histology of the larva otherwise conforms with the general Spionid type, only the remarkable pit is described here. It is an invagination of the ectoderm lying just behind the fold of the contracted lip. The edges are ciliated, but the cavity itself is unusual in that the contents are apparently non-cellular and do not stain. In cross section the pit is reminiscent of a vertebrate notochord. The suggestion that the pit has a sensory function is upheld by its location between the circumœsophageal nerve cords. The first commissures of the double ventral nerve cord (in the second setiger) are shown just behind the pit. Thus the latter is almost entirely surrounded by nervous tissue. The neurotroch in front of the pit is composed of short cilia and commences at the infolding of the posterior lip. There are two groups of strong cilia behind the pit, and it is these that have been referred to as the pit cilia. The third posterior group shown is part of the gastrotroch of the third setiger. It is possible that the function of this organ is similar to that of a statocyst, though no sense organ similar to this is figured in the literature consulted.

Though the shape of the mouth and vestibule remains the same, the œsophagus and rectum are now sinuous in outline, and the stomach-intestine itself is swollen between the septa. The proctodæum is ciliated for a considerable distance internally.

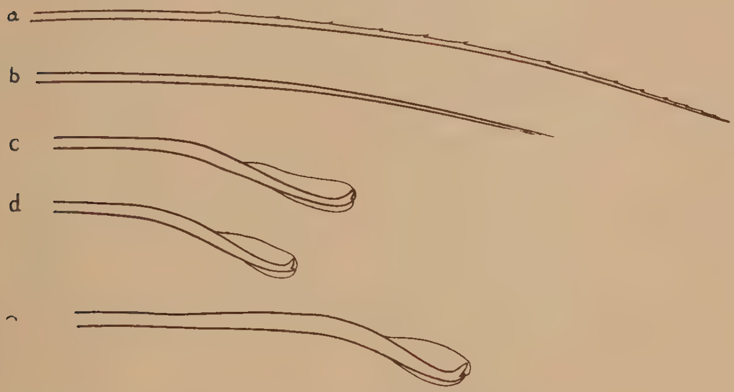

Fig. 14.—(*a*) Larval bristle from a fourteen-setiger larva.
(*b*) Adult type of bristle from the same larva.
(*c*) Crotchet from the 8th parapodium of the same larva.
(*d*) Crotchet from the 10th parapodium of the same larva.
(*e*) Crotchet from the 22nd parapodium of the adult worm.

The parapodia are slightly flattened and there are elongated branchiæ dorsally. In all setigers, with the possible exception of the first, adult setæ (Fig. 14*b*) are present in both the dorsal and ventral bundles. From the eighth setiger onward, crotchets are present in the ventral bundle as well. It is noteworthy that the first crotchets to appear, those in the 8th setiger (Fig. 14*c*) are slightly different from those in the succeeding setigers (Fig. 14*d*), while both are different from the adult type (Fig. 14*e*). The larval bristles (Fig. 14*a*) fall out readily when the animal is trapped on a slide.

The pygidium is short, broad and flattened posteriorly. There are two pairs of anal cirri, which, like the glandular part of the segment and the parapodia, possess tactile cilia. Figure 13 shows a cross section through the anal segment anterior to the anus itself. The large vacuolated cells contain mucus, the limited cytoplasmic contents having large brown chromatophores. These mucus cells, which are themselves ectodermal in origin, open on papillæ which project through the thin ectoderm covering the surface.

From now on growth proceeds slowly and at the end of another week, only a few individuals develop a fifteenth setiger. As will be shown in another paper (Day and Wilson, 1934), experiments were started at this time which show that when kept in conditions unfavourable to metamorphosis larvæ do grow, but so slowly that in another month only four new setigers are added.

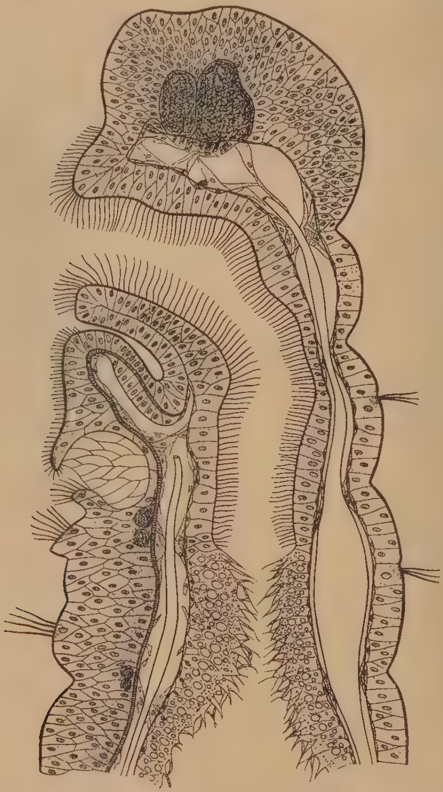

Fig. 15.—Anterior part of a longitudinal section through a fourteen-setiger larva, showing the ciliated pit. × 400.

In the meantime, some of the largest larvæ were put into a vessel containing purified silver sand and filtered sea-water, to which Nitzschia culture had been added. The larvæ were at this time thirty-four days old. Though they at first explored the bottom, they soon started swimming again, showing a preference for the lighted side of the vessel. After twenty-four hours, however, two of the largest attempted without success to burrow below the surface. It was evident that the sand was too coarse.

A finer sandy mud was obtained, purified by boiling, and placed in a finger-bowl, to which the filtered sea-water and larvæ had been transferred. After crawling on the sand for an hour, the larvæ began to burrow below the surface and to metamorphose.

Metamorphosis of the Young Worm.

The actual process of metamorphosis is not easy to follow, since the larvæ first secrete mucus to which sand grains adhere, making observation difficult. These notes are compiled from the examination of larvæ at different stages of metamorphosis. Fortunately the changes cannot be described as "cataclysmic" so that it is possible to obtain a fairly complete picture by removing larvæ from their tubes and trapping them under a cover-slip on a ringed slide.

When a suitable place has been found, the head is bent down, and with its palpi held forward, the larva jerks from side to side, burrowing below the surface. While crawling the larva secretes mucus, by means of which sand grains adhere to the body, but as the larva burrows further sand grains and larval setæ are left behind in a trail of mucus. Not all the larval setæ are lost at once, for those of the first setiger persist till much later.

Possibly under the influence of burrowing, the palpi soon change both in shape and position. The sides of the palpophores grow unequally, so that the palpi are directed forwards, increasing in length and slenderness. Sooner or later the metamorphosing larva constructs a tube of sand grains and debris loosely stuck together with mucus. Here it remains fairly quiet, with its head at the mouth of the tube and the palpi waving freely in the water.

While in this position many changes occur, some gradual, some rapid. A sudden change such as the loss of the gastrotrochs is easily noted, but others such as the gradual development of the antennæ proceed slowly and continuously, so that it is impossible to say definitely whether the antennæ are developed before or after the loss of the gastrotrochs. This point should be held in mind in the perusal of this chapter. Cataclysmic changes—if the loss of the different larval organs can be called such—are recorded in their true succession, but a more correct picture of the metamorphosis is obtained if these superficially striking changes are regarded merely as milestones in the gradual evolution of the adult organs.

Most of the cilia that are functional only during larval existence are now lost. In this category are included the gastrotrochs, the neurotroch and pit, the telotroch and the prototroch. These disappear in the above order, though the telotroch and prototroch persist long after the others have gone. The other groups of cilia, the nototrochs, intersegmental cilia, oral, anal and tactile cilia may change in character but are never lost for they are functional in the adult as well as in the larval stage. The gastrotrochs go first. The actual loss of the cilia is difficult to follow, for when a larva is isolated on a slide for long periods, metamorphosis either stops or proceeds more slowly, and in the meantime plasmolysis takes place. It was ascertained in many cases, however, that when a group of cilia is about to disappear, most of the protoplasm of the cilia is withdrawn into the body of the larva so that a mere wasted shell remains. Whether this falls off or is also absorbed could not be determined with certainty, but it seemed as though a part appreciably shorter than the original was thrown off. The former position of a cilia group can be detected for a few hours by the presence of a paler mark on the surface of the body.

Just before the pit closes, a lump arises on either side, then lengthens out and the depression fills in. The neurotroch is then lost, and within six hours no trace of the pit can be found externally. The prototroch and telotroch, which up to this time are functional when the larva is forced to swim, now disappear. Changes in the shape of the head and the body generally, become visible. The notch in the middle of the prostomium is accentuated and the prominences on either side foreshadow the future antennæ. The lateral lips grow forward, bringing the reduced posterior lip with them, thus covering part of the mouth so that the opening is V-shaped and anterior. The oral cilia are restricted to the sides of the mouth and the surface of the posterior lip. The two dorsal pairs of eyes form a rectangle, the third pair remaining unchanged laterally. The body meanwhile increases in length, becoming more slender and rounded. The pygidium narrows and the anal cirri grow longer.

Twelve hours after the commencement of burrowing the only larval features which remain are the third pair of eyes, the temporary ventral hooks, and the dark pigment of the mid-gut, of the neuropodium of the third setiger, and of the posterior part of the anal segment. These features persist long after metamorphosis is otherwise complete, and disappear gradually in the life of the young worm.

Development proceeds with the further modification of larval structures. The mouth, lips, antennæ, palpi and eyes change in the manner already indicated and soon conform to the adult type. The rami of the parapodia are further flattened, while the branchial portion of the notopodium becomes more distinct. With the lengthening of the setigerous segments, a corresponding change occurs in the pygidium. The two superior pairs of anal cirri grow considerably, but whereas they were colourless from the start, the third pair arising from the division and prolongation of the glandular region of the segment, contain the bluish pigment which characterised it. In the adult worm, however, they can be distinguished only by their larger size. Twenty-four hours after metamorphosis the young worm has reached a stage shown in Figure 16. As there are still differences between this and the adult a brief résumé of its characters is given.

Characters of the Recently Metamorphosed Worm.

The general shape of the body is similar to that of the adult. When forced to swim it does so with a serpentine motion, using its fan-like setæ and flattened parapodia as oars. The young worm is considerably paler and more transparent than the larva, and except for the scattered pigment granules on the head and dorsum, the few dark patches are the remains of the larval pigment. The mid-gut is brown, as is also the neuropodium of the third setiger. The posterior part of the pygidium and the ventral urites are bluish. The bands of yellowish pigment, seen on the palpi of the adult, are not yet developed.

The prostomium is sharply defined. It is roughly oval, slightly notched in front and rounded posteriorly. The antennæ are conical, but soon grow longer and more regularly cylindrical. The palpophores are short, and the palpi which are long, tapered and slightly grooved dorsally, project beyond the antennæ. There are three pairs of eyes, two dorsal, and a lateral pair hidden by the palpophores.

The large lateral lips are protuberant, and curve posteriorly to enclose the V-shaped mouth. There is an indefinite posterior lip and a larger anterior lip that is separated from the laterals by oblique grooves. The opening of the mouth is anterior and ventral, the pharynx is contractile and the œsophagus is thrown into folds by the contraction of the body. The dark stomach-intestine begins about the third setiger and continues till the fourth from the anus; this pigmented part of the gut is characterised by segmental swellings between the septa. Posteriorly the rectum is again folded, and the proctodæum is ciliated for a considerable distance internally.

The lips are beset with short cilia and the antennæ and palpi are sparsely covered with short tactile cilia. In addition there are rows of cilia at the base of the palpi. All setigers except the first, and those that are undeveloped posteriorly have nototrochs and intersegmental groups of cilia. The gills and the anal cirri possess only a few tactile cilia.

The parapodia are of the adult type, but the branchial part of the notopodium is short and does not as yet arch over the dorsum. Both

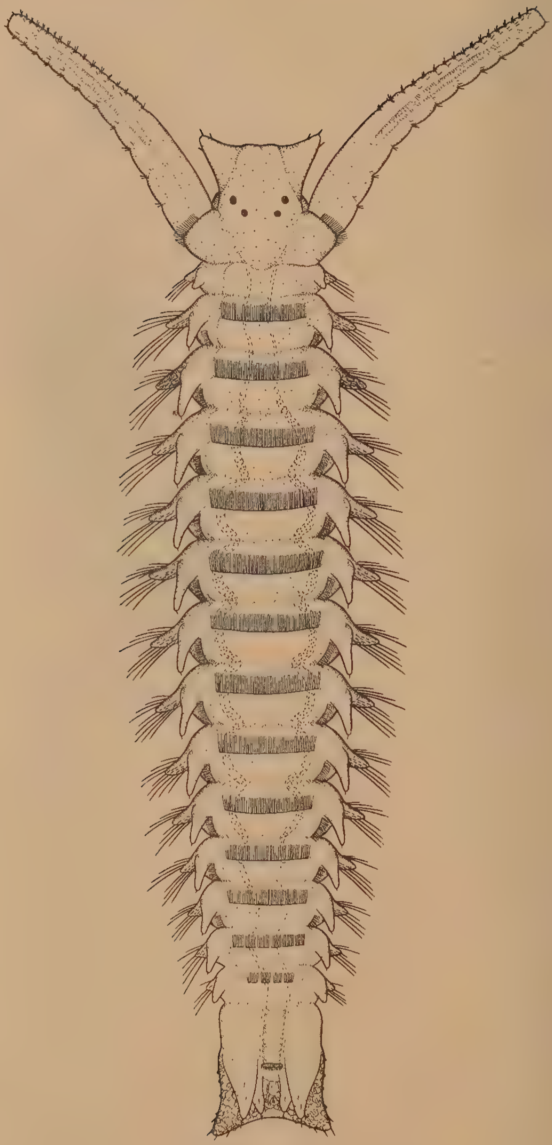

FIG. 16.—Dorsal view of a recently metamorphosed worm. × 104. Actual length 1·367 mm.

the dorsal and the ventral bristle bundles arise on the anterior side of the flattened parapodia and project outwards like a fan. From the eighth setiger onwards, hooded crotchets as well as capillaries are present in the neuropodial group, but these are only temporary, and in the adult crotchets are found only in the twentieth and succeeding setigers.

The pygidium is long and transparent and pigment is restricted to the ventral pair of anal cirri.

From now on the worm grows rapidly. The third pair of eyes are first hidden and then lost. Pigment disappears from the mid-gut, the third parapodia and anal segment. The anal cirri, antennæ and palpi increase greatly in length. As the gills grow longer, they become richly ciliated and arch over the dorsum, and the function of the cilia groups now becomes obvious. Normally the worm rests with its head at the entrance of its mucus-lined tube, the antennæ and long palpi waving freely in the water. In this position there is a free passage between the dorsum and the arched gills, and the motion of the nototrochs, intersegmental cilia and the rows of cilia on the branchiæ draws a current of water down along the dorsum. Part of this current is diverted ventrally at each segment by the action of the intersegmental cilia, thus ensuring a complete circulation of fresh water along the whole length of the body.

SUMMARY.

1. The development of *Scolecolepis fuliginosa* (Claparède) is described from the egg to the young worm for the first time.

2. Comparison of reared larvæ with larvæ from the plankton did not reveal any important difference.

3. The eggs are pelagic, and are similar to those of Nerine.

4. A description is given of the histological structure of a ciliated pit which arises in early larval existence and disappears at metamorphosis. The structure of the glandular region of the pygidium is also described.

5. It is apparent that from the attainment of the fourth setiger onwards, the centre of differentiation is located in the third setiger, so that segmental structures arise first in this segment and then appear in the first and second setigers as well as in the succeeding ones.

6. The larva of Scolecolepis has three pairs of eyes, the third pair disappearing in the young worm long after metamorphosis is otherwise complete.

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On the Relation of the Substratum to the Metamorphosis of *Scolecolepis fuliginosa* (Claparède).

By

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INTRODUCTION.

WHILE investigating the Mitraria larva of *Owenia fusiformis* one of us (Wilson, 1932) obtained striking evidence of the important part played by the nature of the bottom in the metamorphosis of that larva. In the hope that a similar behaviour would be shown by a less specialised type of larval Polychaete experiments were undertaken by us in collaboration. The larvæ used were those of *Scolecolepis fuliginosa.* They were forty days old and were known to be ready to metamorphose given suitable conditions. These larvæ had been reared from the egg by J. H. D., who gives an account of the development in another paper (Day, 1934). Only a limited number were available for experiment but these have proved sufficient to yield a definite result. The major portion of the work was done in the Plymouth Laboratory, but the sands were analysed in the Department of Oceanography, University of Liverpool.

Two initial tests were first made and these giving positive indications that the grade of the bottom deposit is an important factor in metamorphosis a larger experiment was arranged. During these tests a sandy mud had been found in which the larvæ metamorphosed readily. This sandy mud and two other grades of bottom, coarser and finer, were selected and after the first day a fourth grade, a fine clean sand, was also used. A clean glass control dish with rounded corners was included, but it should be noted that in experiments of this kind the ideal control in which the larvæ could not come into contact with any surface whatever is an impossibility.

At the end of the experiment the sands and muds used were examined microscopically (by J. H. D.) and the average size of particles estimated. The sands and muds were then dried and incinerated to obtain a rough estimate of the organic content, which is expressed as a percentage of the dry weight. Care was taken that these results were not falsified by the loss of carbon dioxide from the calcium carbonate present. While it is not suggested that this method of determining organic content is accurate, the results obtained provide comparative values which are important and particularly striking in the mud D.

These results are tabulated below :—

Vessel.	Substratum.	Average diameter of particles.	Limits of variation.	Approximate Organic Content.
A	Smooth glass			
B	Silver sand	0·264 mm.	0·44–0·17 mm.	0·2%
C	Sandy mud	0·047 mm.	0·34–0·03 mm.	6·9%
D	Mud	0·063 mm.	0·15–0·02 mm.	30·0%
E	Fine sand	0·086 mm.	0·10–0·05 mm.	3·0%

The silver sand B consisted of clean well-rounded grains not differing greatly in size. The fine sandy mud C was a mixture of fine particles with organic matter and a few larger sand grains. D was composed largely of organic debris but with a few sand grains, sponge spicules and diatom frustules. E had been elutriated and the variation in size of particle was small. It was dark in colour and contained about 20% calcium carbonate in the form of broken shells. On the whole the grains were sharper and more angular than those of B.

ACCOUNT OF THE EXPERIMENT.

The experiment, details of which are tabulated on page 662, is divided into two parts. The first part extends from noon on April 30th to noon on May 1st, 1933, when certain changes were made and thereafter continues as the second part.

First Part.

Ten larvæ picked at random from the plunger-jar were put into each of four small vessels (30 c.c. capacity) about half-filled with filtered sea-water. These were the vessels A, B, C, and D, and the amount of sand or mud placed in the last three was just sufficient to cover the bottom with a thin layer. If too much is used it is very difficult to find burrowing larvæ when counting. A little Nitzschia was added to the water in the vessels and they were stood on black paper and covered with dark red glass discs to exclude excess light.

In all cases the larvæ explored the vessel, crawling over the bottom and attempting to burrow. If the bottom proved suitable they metamorphosed, otherwise they alternately burrowed and swam. After six hours the only change was in vessel C where all except two had either secreted mucus or metamorphosed. The two swimming larvæ were smaller than the rest and had possibly not reached the stage when metamorphosis can take place. In less than twenty-four hours all the larvæ in C, except the two mentioned, had become young worms, whilst no larva in the other vessels showed any sign of metamorphosis; they were all swimming actively.

Second Part.

The experiment was continued with two objects in view, first to show that the larvæ in vessels A, B, and D were ready to metamorphose, second to determine what eventually happens when larvæ are kept for long periods in conditions unfavourable to metamorphosis.

The 8 young worms in vessel C were removed and 5 of the 10 larvæ in each of the vessels A, B, and D transferred to C. These with the 2 left made a total of 17. The numbers in A, B, and D were made up to 10 by adding 5 fresh larvæ to each. The fifth vessel E containing 10 fresh larvæ was added to the experiment.

At the end of twenty-four hours all the larvæ in C except 4 had metamorphosed. Most of these had changed within three hours, and all but the 4 small larvæ mentioned had burrowed into the sand at the end of five hours. In vessels B, D, and E nothing had occurred, but in A 4 larvæ had metamorphosed. They were, however, unhealthy and soon died.

Since the course of the experiment covers several weeks the account will be more coherent if each vessel is now considered separately for its whole duration. Comparisons may be made from the table. In the accounts the transition from the first to the second part of the experiment may not be specially referred to although it should be borne in mind.

Vessel A. Four larvæ metamorphosed within forty-eight hours. Some diatoms and a little dust had collected at the bottom of the dish and adhered to the mucus tubes of these unhealthy worms which soon died. Meanwhile the 6 swimming larvæ were transferred to a clean vessel A′ where 3 of them became unhealthy and the other 3 were again transferred to a similar clean vessel A″. One of the unhealthy larvæ in A′ died, but the other 2 lived to become abnormal worms, the first at the end of a week, the second after three weeks. These larvæ showed no appreciable increase in size. Of the healthy larvæ in A″ one became a normal worm at the end of a week, a second after eighteen days, while the third died unmetamorphosed after six weeks without showing any appreciable growth.

Vessel B. The first larva metamorphosed on the fourth day. Four of the remaining 9 larvæ were transferred to C′ to see if they would metamorphose given favourable conditions, which they did. Of the 5 left the 2 largest metamorphosed at the end of a week, another 2 within two weeks, and the last within three weeks. All worms were healthy and lived for a considerable time.

Vessel C. At the end of the first day 8 larvæ had metamorphosed. The 8 worms were removed and 15 swimming larvæ (5 from each of vessels A, B, and D) added. Twenty-four hours later all but 4 of the 17 larvæ had metamorphosed and these did so four days later. The young worms were sent to Liverpool on May 12th. Half of them survived the journey, and 6 were still alive at the end of three months, when they varied in length from 3 to 14 mm. The largest had lost all larval characteristics, but the smaller ones still retained the larval pigment in the anal cirri and third parapodium.

Vessel C′. This had the same kind of bottom as C and was used to test whether larvæ in vessels B and E could metamorphose. When larvæ were transferred from these vessels on May 3rd three were unfortunately lost. Five out of the remaining 6 metamorphosed within three days and the last by the seventh day. Later 2 larvæ were transferred from E and they immediately began to metamorphose.

Vessel D. Three larvæ died on the third day. On the same day 2 metamorphosed followed by 2 more the next day. At the end of the first week there were 6 worms and 1 larva. Two days later this larva had also metamorphosed.

Vessel E. As there was no change after forty-eight hours 5 of the larvæ picked at random were transferred to vessel C′ where they soon metamorphosed. The remaining 5 still showing no change at the end of a week another 2 were then tested. These also metamorphosed in C′. No larva metamorphosed in E until the end of the third week when 2 of the remaining 3 larvæ became young worms. The last larva was transferred to a similar vessel E′. For nine weeks this individual appeared to be in perfect health, sometimes resting on the bottom, sometimes swimming vigorously. At the end of this period it underwent what seemed to be an attempt at metamorphosis during which it became unhealthy and died. These last three larvæ all grew and gained new setigers, the first two metamorphosed with 16 and 18 setigers, and when the last one died it had between 18 and 20 setigers.

DISCUSSION.

It is evident from these results that the muddy sand in vessel C was a very suitable bottom for metamorphosis. This muddy sand was of a very similar nature to that in which the adult worms are found. The silver sand in B and the mud in D were evidently not so suitable ; there was a delay before the larvæ metamorphosed. Since the larvæ were taken at random from the plunger-jar there is only a very slight possibility that those in C were more advanced than those in the other vessels. This possibility is, however, discounted by the result obtained when larvæ from B and D were transferred to C at noon on May 1st. Conclusive evidence of delay on an unsuitable bottom is however furnished by vessel E where there is no possibility of explaining the results there obtained by assuming that the larvæ were in any case not quite ready to undergo their critical change. The delay is far too great and moreover by the time the last three larvæ metamorphosed or died they had more setigers than the stage at which the larvæ first come into a condition when metamorphosis is possible. The larvæ tested by transference to a suitable substratum on the three dates, May 1st, 3rd, and 10th gave as good a proof as could be obtained that the larvæ in this dish were ready to metamorphose during the whole period. Why two of them actually metamorphosed on this bottom on May 22nd is not clear, but the fact that they did so successfully and continued to grow until they were fixed over a month later demonstrates that the bottom itself was not an impossible one for the young worms to live in, at least under laboratory conditions. During this time one had attained 72 setigers and the other 48. The only larval features that remained were the pigment patches on the third parapodia and the anal cirri, as the third pair of eyes had disappeared and the hooded crotchets did not commence till the 23rd setiger. On the shore adults of this species are to be found rarely, if at all, in fine clean sand of this nature.

It is interesting to note that the sand in vessel E which proved so unattractive to Scolecolepis larvæ was of the character that would have readily induced metamorphosis in the Mitraria larva of *Owenia fusiformis*, while the muddy sand in vessel C would probably have proved unsuitable for that species.

Vessel A yields little information. As remarked above it is not an ideal control. We are unable to explain why some of the larvæ became unhealthy after the first two or three days.

General Conclusions.

While admitting that it would have been desirable to have used a larger number of larvæ had they been available we are of the opinion that it is possible to draw conclusions of considerable ecological interest. These are as follows :—

1. *Scolecolepis fuliginosa* larvæ do not metamorphose until they have reached the fourteen-setiger stage attained after six weeks of free swimming existence assuming the rate of development in the sea to be the same as in the laboratory.

2. When this stage is reached they make their way to the bottom and begin to burrow as soon as suitable ground is found.

3. They do not metamorphose in the plankton in mid-water and then sink to the bottom to take up adult life.

4. Metamorphosis may be complete in twelve hours or less.

5. The suitability of the substratum evidently depends to some extent at least on the grade of the bottom deposits, a sandy mud being most suitable. Other factors, such as the organic content, may also determine the suitability.

6. Should a suitable locality not be found immediately the larva is able to postpone metamorphosis for a period that may be as long as several weeks. In the meantime the larva still actively swimming, grows slowly with the addition of new setigers.

7. If the right kind of ground is never reached an attempt is made at metamorphosis which may or may not produce a normal worm. This point is not clear and needs further investigation.

8. This ability to delay metamorphosis must greatly increase the larva's chance of reaching suitable ground, and is therefore of the utmost importance as a survival factor.

Apart from those details that are obviously specific for *Scolecolepis fuliginosa* these conclusions are in the main the same as those already formulated for the Mitraria larva (Wilson, 1932, p. 309). They are probably general for other species as well. The account one of us has given of the settling down and metamorphosis of the very similar larva of *Polydora hoplura* (Wilson, 1928b, pp. 583–585) is very suggestive that these postpone metamorphosis until they have found a suitable crevice in which to settle and begin adult life. Species that when adult are sedentary attached to rocks, shells, etc. (e.g. Pomatoceros, Sabellaria) may also suspend metamorphosis for a while until they reach some hard object on the sea bottom. In such cases, however, it would be exceedingly difficult to devise laboratory experiments to show this, as the side of any containing vessel is a suitable substratum for such larvæ. Worms that have a post-larval pelagic stage in a secreted tube (Lanice, Loimia, Arenicola, Pectinaria) will almost certainly be able to live and grow for some time after the stage at which they would normally become benthonic. Monro records (1930 and 1931) some interesting specimens of pelagic Loimia worms belonging, apparently, to the species *L. medusa*, especially one that was obtained between 250 metres and 100 metres in the middle of the South Atlantic. This specimen was at a much more advanced stage than that at which young pelagic *Loimia medusa*, given the opportunity, will start building their sandy tubes (Wilson, 1928a). Probably this worm had failed to reach the bottom at the usual time but had continued to grow normally in spite of an unusually long pelagic existence.

It is hoped to continue investigations along these lines whenever opportunity permits. It is scarcely necessary further to stress the ecological importance of such observations and their bearing on the distribution of ocean life.

SUMMARY.

Laboratory experiments indicate that larvæ of *Scolecolepis fuliginosa* when ready to metamorphose, are able, if necessary, to postpone metamorphosis until a substratum suitable for adult life is reached, meanwhile continuing to swim and grow for a period that may be as long as several weeks.

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EXPLANATION OF THE TABLE.

The main results of the experiment are here tabulated to facilitate comparison between the time of metamorphosis in the different vessels. Only essential dates are recorded. The following abbreviations are used :—

a, abnormal. b, burrowing larva beginning to metamorphose. d, dead. l, accidentally lost. s, swimming larva. u, unhealthy. w, young metamorphosed worm.

The following symbols denote changes in the different vessels.

* 5 larvæ removed to C and 5 fresh swimming larvæ added.

[1] 8 worms removed.

[2] 15 larvæ, 5 from each of A, B and D were added, making with the 2 already present a total of 17.

[3] 6 larvæ transferred from A to A′.

[4] 3 healthy larvæ transferred from A′ to A″.

[5] 4 larvæ transferred from B to C′.

[6] 5 larvæ transferred from E to C′.

[7] 2 larvæ transferred from E to C′. They started to burrow immediately.

[8] 1 larva transferred from E to E′.

[9] Contents of the vessel sent to Liverpool. On arrival 8 worms were still living.

Date.		A Clean Vessel.	A′ Clean Vessel.	A″ Clean Vessel.	B Silver Sand.	C Sandy Mud.	C′ Sandy Mud.	D Mud.	F Fine Sand.	F′ Fine Sand.
April 30	Noon	10s			10s	10s		10s		
,,	1.30 p.m.	,,			,,	2s, 8b		,,		
,,	6 p.m.	,,			,,	2s, 5b, 3w		,,		
May 1	10 a.m.	,,			,,	2s, 8w^1		,,		
,,	Noon	10s*			10s*	17s^2		10s*	10s	
,,	1 p.m.	,,			,,	13s, 4b		,,	,,	
,,	2.30 p.m.	,,			,,	10s, 7b		,,	,,	
,,	5 p.m.	,,			,,	4s, 13b		,,	,,	
,, 2		6s^3, 4uw	6s^3		,,	4s, 13w		,,	,,	
,, 3		4dw	3s^4, 3us	3s^4	9s^5, 1w	,,	4s^5, 5s^6	5s, 2w, 3ds	10s^6	
,, 4			2us, 1ds	,,	5s, 1w	,,	2s, 2b, 2w, 3l	3s, 4w	5s	
,, 6			,,	2s, 1w	3s, 3w	17w	1s, 5w	1s, 6w	,,	
,, 8			1us, 1aw	,,	,,	,,	,,	7w	,,	
,, 10			,,	,,	,,	,,	6w, 2b^7	,,	5s^7	
,, 12			,,	,,	,,	8w^9	8w	,,	3s	
,, 15			,,	,,	1s, 5w	,,	,,	,,	,,	
,, 19			,,	1s, 2w	6w	,,	,,	,,	,,	
,, 22			2aw	,,	,,	6w, 2dw	,,	?	1s^8, 2w	1s^8
,, 29			,,	,,	,,	6w	,,	Dead	2w	,,
June 6			2dw	1us, 1w, 1dw	,,	,,	7w, 1dw		,,	,,
,, 11				Dead	?	,,	?		,,	,,
,, 28					2w, 4dw	,,	Dead		2w	,,
July 3						,,				1ub
,, 4						,,				,,
,, 26						6w				

The Habitat of *Procerodes ulvæ*.

By

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The relation of *Procerodes ulvæ* (*Gunda ulvæ*) to its environment has recently been studied by Pantin. In a series of papers (Pantin, 1931 (1) and (2); Weil and Pantin, 1931) a number of interesting facts have been brought out, which can be summarised as follows: This turbellarian is one of a very small number of marine forms which successfully colonise a region where there are large abrupt changes in osmotic pressure. It is found under stones in the intertidal zone and mainly where a stream of fresh water flows down the beach, though it occurs elsewhere too. In this habitat it is immersed in sea-water at high tide but between tides it is in perfectly fresh water (less than 0·01% sea-water). Procerodes is not water-tight, but swells up in fresh water. The swelling is controlled, however, and the animal loses salts in the process. The animal does not come into osmotic equilibrium with fresh water, as it does with sea-water, but can maintain a "steady state" for a time by means of an increased expenditure of energy as shown by increased oxygen intake (Beadle, 1931). The steady state is much better maintained and the swelling controlled in the presence of an appreciable concentration of calcium salts. The particular stream examined by Pantin, at Wembury near Plymouth, contains 58–65 mgm. of calcium per litre. For comparison sea-water contains 420 mgm. Ca per litre. Very hard spring water may contain as much as sea-water, while upland surface water may contain as little as 1 or 2 mgm. per litre.

The question now arises, is Procerodes confined to regions of hard water streams or if it lives in soft water streams is it driven further down the beach, where it has a shorter interval in fresh water? With a view to answering this question I have examined many miles of coast in different parts of the country and, though I never failed to find Procerodes wherever conditions were suitable, for a long time I failed to find a soft water stream on the coast. Whatever the nature of the underlying rock, surface water from cultivated land contains 20 mgm. or more of Ca per litre, generally more. The amount will vary of course with the weather, time of year, and treatment of the soil, and immediately after heavy rain may sink to quite low values. Even where there is no cultivation concentrations between 10 and 20 mgm. are likely. But lower values have been found in two regions, one in the Isle of Man, the other in Morar, Invernesshire.

Place.	Date.	Calc. mgm. per litre.
West of St. Ives, Cornwall (2 streams)	15.7.32	12, 15
St. David's Head, Pembroke	2.7.31	14
South of Carmel Head, Anglesey (2 streams)	13.9.32	17, 18
Bay Fine, Southern end of Isle of Man	8.4.32, 24.9.32	19, 16
Bay Stacka ,, ,, ,, ,,	10.4.32, 25.9.32	18, 13
Near Fleshwick Bay, W. coast of Isle of Man	18.5.33	6
The Stacks, W. coast of Isle of Man	24.9.32, 17.5.33	5, 4
Loch nan Ceall, Morar	19.8.33	5
Bourblach House ,,	19.8.33	5
Sgeir Mhor ,,	19.8.33, 13.9.33	5, 12
Boagha Dearg ,,	13.9.33	8

None of these waters were acid. The Morar waters, though coming from deep peat and coloured with it, were alkaline (pH 7·2 to 7·6) and had an appreciable alkali reserve (combined CO_2). This is presumably the result of active vegetation ; in winter the results might be different. The nearest approach to pure water is that found at The Stacks, Isle of Man. This place is perhaps worth a fuller description.

About 3½ miles north of Port Erin a stream is marked on the One-Inch Ordnance Map entering the sea near a point marked " The Stacks." The stream drains quite uncultivated land, covered with a scanty growth of heather and gorse. The soil is thin and somewhat peaty. The stream drops 500 feet in the course of a quarter of a mile. About half-way down it falls over a small cliff into a shallow ravine where there is much loose soil and stones. Above the ravine the water was found to contain 2–3 mgm. Ca per litre, at the beach 4–5 mgm. Evidently it picks up some from the soil on the way down. The beach is sheltered by outlying rocks and consists of large stones. It is an excellent habitat for Procerodes, which is abundant at all levels.

There is another more accessible stream with low calcium content near Fleshwick Bay, but here the upper beach is shingle and devoid of life so that Procerodes is confined to the lower levels. The Morar beaches are more accessible and have the advantage that High Water at Neaps occurs at less awkward times of day than in the Isle of Man. Observations of the upper limit of Procerodes have been made in both places but before discussing them something ought to be said about what in general constitutes a suitable habitat.

Procerodes lives on the undersides of stones that are large enough or well enough imbedded to be seldom moved. But it needs clean well aerated conditions so that the underside should be on rock, gravel, or coarse sand. Consequently it is scarce or absent in really sheltered waters where the beaches are usually muddy. It is always to be found on beaches of the open coast where the conditions are suitable. In general the best habitat is where the stream is small so that there is not enough flood water to move stones about and where it runs down a gully in rocks or down a beach of large stones in a cove with some shelter from outlying rocks or big boulders. I have found Procerodes flourishing at an exposed part of the southern coast of the Land's End peninsula, where there is a " beach " of huge granite boulders firmly pounded and wedged together by the seas. Underneath the boulders are pools with stones and coarse gravel evidently quite sheltered from the heavy seas of this coast.

On many beaches the higher part from the level of Spring High Water down to the Neap High Water level or lower is shifting gravel or shingle where nothing can live, so that only the lower part of the beach is suitable for Procerodes and other intertidal forms. Where there is a question of the upper limit of Procerodes it is necessary to consider only places where the upper zones are physically suitable.

It is noticeable that, where a stream runs down, the beach is cleaner and less liable to contain putrefying algal detritus. This fact and the fact that the stream keeps things cool and moist makes the region of the stream a better habitat in other respects than the rest of the beach for an organism that can endure large osmotic changes. In the middle of the tidal zone Procerodes is often to be found well away from the stream but higher up it is confined to it. Elsewhere the underside of stones high up the beach will dry up and warm up between tides and may be sticky with decayed weed. Gammarus and a few Isopods can flourish there but nothing else.

Pantin (1931, 1) found Procerodes at Wembury living up to about the level of High Water Neaps, and it was clear from an examination of many beaches that the upper limit is somewhere in this region, but further observation was evidently necessary. When I examined the beach of the Stacks, I.O.M., at Neap High Water of May 17th, 1933, it was surprising to find that the highest Procerodes were more than a foot above the highest point reached by the sea. There was a light offshore wind and the splash zone was quite small. By approximate calculation from the tide tables it was clear that on this beach the uppermost Procerodes were liable to be in pure stream water containing only 5 mgm. Ca per litre for 3 days, possibly 5 days, if there was calm weather with a Neap Tide period, and it had been seen that they could stand at least 2 days without harm. In rough weather of course they would always get splashed. Observations were also made at Bay Stacka using a tape dyed with silver chromate which is stained white by salt water. The highest Procerodes there were at a similar level above high water and they were found alive after 3 days without sea-water in water containing 13–18 mgm. Ca per litre.

It was noticed on these two beaches that the upper limit of Procerodes was very close to the upper limit of *Fucus spiralis* on adjacent rocks. As the line is very sharp and as the upper limit of *Fucus spiralis* is also the lower limit of *Pelvetia caniculata* these two weeds provide an excellent point of reference which may be taken as marking the same tidal level on all beaches, i.e. about Mean High Water Neaps (Colman, 1933).

The Morar coast was visited in August, 1933, and a region for observation was found on the coast below Bourblach Hill to the west of the road to Mallaig just north of the estuary of Morar River (*cf.* One-inch Ordnance Map). This region is entirely uncultivated and the soil is peat. It contains several small streams, of which two are specially suitable. One just north of Sgeir Mhor runs down a cleft in the rocks forming shallow pools with stones. The other is further north, by Bogha Dearg, where a stream is marked on the map. This stream runs down a very gently shelving stony beach sheltered by outlying rocks. A third stream running into the Morar estuary just below Bourblach House with some slight cultivation on its course, was also examined. Although in shelter the beach is clean and suitable for Procerodes. In this region Procerodes is not abundant but is found in all suitable places, the upper limit was seen to be very close to that of *Fucus spiralis* in all three places.

Further observations were made at the low Neap Tides in September (lowest on September 13th). From the data in the Admiralty Tide Tables it is clear that the predictions for Stornoway can be applied to this coast without appreciable correction for height. Fortunately there was a spell of fine weather with calm sea and mainly offshore winds at this time, so that the splash zone was small.

At all three stations the upper limit of Procerodes coincided very closely with that of *Fucus spiralis*, it was certainly not lower. The high water of the afternoon of the 13th (9·4 ft.) was more than a foot below this line at Sgeir Mhor and that of the afternoon of the 14th (10·0 ft.) at least a foot below at Sgeir Mhor and Bogha Dearg. The morning tide of the 14th was predicted as 9·2 ft. so that it was not necessary to make an observation of it. The morning tide of the 15th (9·9 ft.) was observed at Sgeir Mhor by means of silver chromate tape. The wind was S.W. and freshening, raising some sea. Although the splash zone was now considerable the highest Procerodes pool cannot have been reached by sea-water. On this morning (September 15th) the Procerodes at Sgeir Mhor and Bourblach House, which cannot have been in sea-water since the night of September 10th to 11th (10·8 ft. tide) and possibly not since the previous night, were mobile and apparently in good condition if a little swollen. There was no time to visit Bogha Dearg again, but the Procerodes there were alive on the afternoon of the 14th. The afternoon tide of the 15th (10·8 ft.) almost certainly covered the whole Procerodes zone, with the onshore wind then blowing, but if the weather had been calm might have barely reached the upper limit.

It was disappointing to find that the calcium content of the Morar waters was higher than in August, presumably owing to the dry weather. However, the quantities, 8 and 12 mgm. per litre, were not excessive.

For comparison with Morar, the coast to the east of St. Andrews Bay, Fife (Kinkell Braes), was examined on September 11th. A number of small streams partly from springs in the sandstone and partly drainage of cultivated land occur here. In many places the upper beach is pure shell sand and not suitable for Procerodes, but one excellent place was found just west of Kinkell Ness. The water here contained 39 mgm. Ca per litre and Procerodes was living up to the line dividing *Fucus spiralis* and *Pelvetia caniculata.* By reference to these algæ there was no perceptible difference between the upper limit here and in Morar, or in fact in any region examined.

It must be concluded (1) that Procerodes is not limited in its distribution by the calcium content of the fresh water stream it colonizes down to a minimum of 5 mgm. Ca per litre : (2) that it can survive about 5 days without sea-water, a contingency that may occur whenever a low neap tide period coincides with calm weather. It has been pointed out by Orton (1933) that the combination of neap tides, calm sea, and hot weather may be very lethal to the population of the upper part of the tidal zone (i.e. above the lowest Neap High Water level). The habitat chosen by Procerodes has at least the advantage that it is never exposed to high temperature or dessication, and the animal is not confined to short and uncertain periods of immersion in sea-water for obtaining its food.

In the laboratory Procerodes does not seem able to survive more than about 2 days in pure water ; but it must be remembered that laboratory conditions are probably much severer than its natural habitat on account of high temperature, exposure to strong light, and absence of food supply. So that it is not altogether surprising that it should succumb more quickly.

SUMMARY.

Procerodes ulvæ has been found living in streams with calcium content as low as 5 mgm. per litre. Its upper limit does not appear to be affected by the calcium content of the water. The animals at the upper limit are liable to about 5 days' exposure to fresh water if calm weather coincides with Neap Tides. Animals living in water of 8–12 mgm. Ca per litre have been found alive at the end of such a period.

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Two Parasites of the Common Cockle *Cardium edule;* a Rhabdocoele *Paravortex cardii* Hallez and a Copepod *Paranthessius rostratus* (Canu).

By

D. Atkins, B.Sc.

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IN view of the serious mortality reported among *Cardium edule* in the summer of 1933 (Orton) the following account of British parasites of this species may be of interest.

PARAVORTEX CARDII HALLEZ.

Apparently healthy cockles in the Plymouth area are very generally infected with a viviparous Rhabdocœle, *Paravortex cardii* Hallez (Hallez, 1909). In a passing reference to this parasite in a recent paper (Atkins, 1933, p. 250) I incorrectly referred to it as *Graffilla gemellipara* Linton, a species known as a commensal of *Modiolus demissus* at Woods Hole, America (Linton, 1910).* While my paper was still in the press, but too late for correction, I chanced upon Hallez's paper on *Paravortex cardii*, a species of Rhabdocœle parasitic in *Cardium edule* from Le Portel, Boulogne-sur-Mer. Examination of the parasite of cockles from the Plymouth area showed it to be this species, and not *Paravortex* (=*Graffilla*) *gemellipara* (Linton).

The characteristics of *P. cardii* as given by Hallez (1909, pp. 430–1) are as follows : " Vorticide pourvu de deux ovaires, de deux glandes lécithogènes réticulées et anastomosées et de deux testicules globuleux ; dépourvu de bourse séminale. Orifice génital ventral situé près du pharynx en arrière, à l'extrémité du premier quart du corps. Organe copulateur mâle musculeux, dépourvu de pièces chitineuses et portant deux lobes papillifères. Pharynx doliiforme. Bouche ventrale vers l'extrémité antérieure du corps. Corps cylindrique, à extrémité antérieure plus amincie que le reste du corps, uniformément cilié, blanc légèrement jaunâtre, transparent, dépourvu de rhabdites, très contractile, ordinairement courbé en arc et tournant sur place en décrivant un cercle. Deux yeux noirs réniformes au niveau du pharynx. Longueur maxima, 1 mm.; largeur, 0·3 à 0·4 mm. Vivipare. Nombreuses coques molles (jusqu'à 40) renfermant chacune un à quatre embryons et disséminées dans le tissu conjonctif. Les coques vides et recroquevillées restent dans le corps de la mère. Vit dans l'estomac du *Cardium edule.*"

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* Leigh-Sharpe (1933) in a note on the occurrence of a Turbellarian in a *Cardium edule* from Millbrook, Plymouth, also appears to have wrongly identified it as *Graffilla gemellipara*. The animal he figures has the appearance of being somewhat compressed.

The reproductive organs, so far as can be seen in the living animal, are on the plan described and figured by Hallez (1909, Pl. XXVII, Fig. 20). The atrium was rarely distinguished satisfactorily. The general presence of sperm in the female atrium and oviducts and in the vesicula seminalis renders these parts of the generative apparatus clearly visible; when empty, however, the female atrium and oviducts are distinguishable with difficulty.

Ball in 1916 (p. 455) added to Linton's description of the Rhabdocœle commensal with *Modiolus demissus*, and (p. 459) referred it to the genus Paravortex. He (pp. 459–60) sums up the likenesses and differences of the two species as follows: "Linton's species and *P. cardii* are closely similar both in structure and habits. Both have essentially the same colour and the same shape of body. Both have similar digestive, sensory and glandular organs; both give birth to living young which develop in capsules within the mother's body; both show the same peculiar movements when taken from their host and placed in sea-water.

"The two species differ, however, in that the American form attains twice the size of *P. cardii;* the genital pore is situated farther posteriorly and the ovaries are longer in the latter;* an atrial canal in *P. cardii* leads from the dorsal part of the atrium backward to the antrum femininum, while in the American species there is no distinct canal but rather the antrum femininum extends backward from the middle of the posterior atrial surface and its opening into the latter is strongly constricted by a sphincter muscle; the openings of the shell glands in *P. cardii* are distributed along the entire ventral wall of the atrial canal and antrum femininum, while in Linton's species they all open at the anterior end of the antrum just back of the atrium; the vitello-oviducts of *P. cardii* are the longer. Linton's species lives as a commensal in the mantle cavity of the ribbed mussel, *Modiolus demissus ; P. cardii* is parasitic in the stomach of *Cardium edule.*

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* This is evidently an error for "former," for the genital opening of *P. cardii* is at the end of the first quarter of the body (Hallez, 1909, p. 431); that of *P. gemellipara* is at the end of the first third (Ball, 1916, p. 455).

"Linton's species resembles *Paravortex scrobicularia* rather than *P. cardii* in the form of the ovaries, i.e., they are elongated in the first two and shorter in *P. cardii.*"

Linton (1910) the discoverer of *P. gemellipara* stated that it was a commensal, but Patterson (1912, pp. 174–5) concluded that it lived chiefly in the kidney. Ball (1916, pp. 462–3), however, failed to find any evidence that it was other than a commensal.

Occasionally specimens of *P. cardii* from Cardium from the Plymouth area are somewhat larger than the maximum length given by Hallez, reaching at least 1·2 mm., but measurements are difficult to make owing to the animals being very contractile, and no really satisfactory narcotic being discovered. Cocain—used by Hallez—was not obtainable ; stovain and chloretone were not successful ; isotonic magnesium chloride gave fairly good results, but caused shedding of the ectoderm in a short time. The maximum length of *P. gemellipara* is given as 2·0 mm. (Linton, 1910, p. 372).

The greatest number of capsules containing embryos observed by Hallez in a single individual was 40. However, a specimen, about 1·2 mm. long, from a Yealm Estuary Cardium, contained 47 full capsules (20 with embryos with eyes developed), while one from Neille Point had 50 to 60 full capsules, many with embryos with eyes developed. Capsules with more than 2 embryos have not been observed, though some 30 capsule-containing specimens have been examined.

According to Hallez (1909, pp. 438, 446) the adult parasites are always found in the stomach of their host. The embryos escape from the body of the parent and pass into the intestine of the host, where they attain their development in some three or four days (this being the time necessary for the emptying of the gut in cockles deprived of food) and pass out by the exhalent siphon. He believes that copulation takes place normally in the intestine, but perhaps exceptionally during the free-living period. Immediately after copulation there occurs migration into the stomach of another Cardium, where the parasite completes its life history.

Hallez (1909, pp. 438-443) notes that exceptionally the formation of capsules may begin while the Rhabdocœle is in the intestine of the host. While the intestines of few Cardium were examined at Plymouth, it was found that of 14 Paravortex, the largest of which was about 0·9 mm. long, taken from this position from 5 hosts, 7 contained 1 to 10 capsules.

The quantity of sperm in the female atrium and oviducts of young specimens is frequently much less than in large ones with many capsules : it would seem, therefore, that copulation occurs more than once, unless self-fertilisation takes place as Hallez supposed possible (1909, p. 444). It is of special interest that a Paravortex from a Neille Point cockle was crowded with numerous capsules the contents of which were degenerating. It seems probable that this was due to the ova being unfertilised; the only sperm visible was a minute quantity of immobile sperm in the vesicula seminalis.

Distribution in the Plymouth Area.

Estuaries of the Hamoaze. Infected cockles have been obtained from several localities.

(*a*) Millbrook. Of those procured on October 12th, 1933, the stomachs of the ten examined were all infected with Paravortex; the intestines were not examined. Single individuals were found respectively with: 27 parasites, all small and none carrying embryos; 23 (7 with capsules); 20 (6 with capsules); 14 (12 with capsules); 10 (4 with capsules); 4 (one being large, with many capsules, and 3 tiny); while four individuals contained two each (all with capsules). A peculiarity of this batch was the number of small individuals.

(*b*) St. John's, St. John's Lake. Three small cockles, 11·0 to 18·0 mm. long, gathered on July 27th, 1933, proved to be infected. From one of these thirteen Paravortex were taken, four having 1 to 14 full capsules. Six of them, including one with 4 capsules, were taken from the intestine. The second Cardium yielded nine parasites, 4 carrying 1 to 4 full capsules. Two of them, each with a single capsule, were taken from the intestine. From the third Cardium eight Paravortex were taken, only one having capsules (8); a tiny one came from the intestine.

(*c*) Saint German's on the Lynher River. Twelve out of fourteen cockles (85·7%) obtained on August 25th, 1933, proved to be infected. The stomachs were examined but not the intestines. Five cockles had one Paravortex each—one being also infected with the sporocysts and cercariæ (Bucephalus) of Gasterostomum;—one had 3; one had 4; one had 5; two had 7; and one had 11.

(*d*) Neille Point, near the junction of the Tamar and Tavy. Four out of ten Cardium (40%) examined on August 3rd, 1933, proved to be infected, one large Paravortex being taken from the stomach of each (the intestines were not examined). The number of full capsules present in these individuals was 22, 26, 50 to 60; in one they were too numerous to count.

(*e*) Stonehouse Pool. Twelve out of thirteen cockles (ca. 92%), examined on August 8th, 1933, were infected. The stomachs only were examined: five individuals had 1 parasite each; one had 3; one had 4; two had 5; one had 6; one had 8; and one had 14.

Yealm Estuary. Cardium from this locality are very generally infected;

of five small individuals especially examined in July, 1933, four were parasitised. Details of the infection are as follows: From one cockle, 23 Paravortex were obtained, 3 only being without capsules. The number of full capsules varied from 3 to about 30 in different individuals, 13 having 10 or more. Escaped young were found in the watch glass with these adults. Seven specimens were a millimetre and more in length. From a second Cardium 17 *P. cardii* were taken, 11 having 2 to 16 full capsules. Five individuals were a millimetre and more in length. From a third Cardium 7 parasites were taken, 3 with 1 to 10 full capsules. Two were a millimetre and more long. From a fourth cockle 3 parasites were taken. Of two, about 1·2 mm. long, one had 47 full capsules, the embryos of 20 having eyes already formed, and the other 31 full capsules, 17 containing embryos with eyes formed. The third specimen, about 0·9 mm. long, had 2 capsules with young embryos.

Salcombe Estuary. Parasitised cockles have been obtained from Kingsbridge. Four out of seventeen (ca. 23%) examined from this locality on August 11th, 1933, were infected. The number of *P. cardii* in a host was small, 3 having 2 each and the fourth a single specimen.

From Millbay, near the mouth of the Estuary, 6 cockles, gathered from the surface on September 5, 1933, had no Paravortex. One at least had the interlamellar spaces of the gills swarming with an Ancistrum type of Ciliate.

From these few examples it would seem that infection varies considerably in different localities, being heaviest in cockles from Millbrook, St. John's Lake, St. German's, Stonehouse Pool and the Yealm Estuary. From these five localities 31 out of 41 hosts had more than one parasite, and one had as many as 27. The infection is heavier than Hallez found at Le Portel, for he writes (1909, p. 437): " Il est à noter que le nombre des Cardium qui n'hébergent qu'un seul individu est très élevé (43 à 52%) et qu'il est relativement rare de trouver plus de quatre parasites dans le même estomac."

P. cardii would seem to have a wide distribution in the British Isles. Nicoll (1906, p. 154 and Pl. IV, Fig. 7) described as a Trematode sporocyst in *C. edule* at St. Andrews, Scotland, a form which is almost certainly this Rhabdocœle. Dr. M. V. Lebour, to whom I am indebted for the reference both to Linton's and to Nicoll's paper, has pointed out to me that she (1904, pp. 83–84) also described as a Trematode sporocyst in *C. edule* from Budle Bay, Northumberland, a form which is no doubt identical with the Rhabdocœle from South Devon and Cornwall. Lebour (1904, pp. 83, 84) found the parasite in about 75% of the cockles examined. Nicoll (1906, p. 154) states: " Rarely were there more than half a dozen in one cockle, and only in about 20% were they entirely absent." Hallez (1909, pp. 435, 436) found at Le Portel, Boulogne-sur-Mer that 141 out of 300 (47%) *C. edule* examined during August, September, October and November were infected, the number of parasites in a host varying from one to twenty ; 43% contained one only. In December about 43% were infected ; in February about 46%. He therefore concludes that the winter has no influence on the percentage, which remains very much the same as during the summer and autumn. Analogous results were obtained in the spring. At Dannes-Camiers he found the percentage infected to reach 67%.

PARANTHESSIUS ROSTRATUS (CANU).

Paranthessius (=*Herrmannella*) *rostratus* (see Canu, 1892, pp. 235–7, Pl. XXIV, Figs 1–13 ; Monod and Dollfus, 1932, pp. 143–6) has been obtained from the mantle cavity of Cardium from several localities in the Plymouth area. From Neille Point, near the junction of the Tamar and Tavy, the mantle chambers of ten cockles examined on August 3rd, 1933, were aswarm with the copepod. Thirteen cockles from Stonehouse Pool on August 8th, were all infected with Paranthessius, but not heavily. Fourteen Cardium obtained from near Saint German's on the Lynher River, on August 25th, all proved to be heavily infected : females carrying egg-sacs were numerous. Ten cockles examined of those obtained from Millbrook on October 12th were all infected : some of the adults carried egg-sacs.

From Kingsbridge on the Salcombe Estuary seventeen cockles, obtained on August 11th, were all rather heavily infected : many of the copepods carried egg-sacs. On September 5th six cockles from Millbay, near the mouth of the estuary, all proved to be infected : some of the copepods carried egg-sacs.

This copepod was first recorded in the British Isles from *C. edule* from Morecambe Bay, Lancashire, by Fraser (1932). Leigh-Sharpe (1933a, pp. 113–4) has since recorded it from the testis of Cardium from Millbrook, near Plymouth.

Paranthessius is a semi-parasite only (see Canu, 1892) and has been taken in tow-nettings from gulleys on the cockle beds in Morecambe Bay by Fraser (1932).

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Studies in Sublittoral Ecology. I. A Submarine Gully in Wembury Bay, South Devon.

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With 2 Figures in the Text.

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I. INTRODUCTION.

BOTH the intertidal region of the shore, and the sea-bottom at depths of anything over three or four fathoms, have been comparatively well explored biologically; but that part of the sea coast which lies just below the level of low water spring tides is—around the British Isles—almost unknown. It is out of range of ordinary shore-collecting, and yet much of it is also unsuitable for detailed investigation from a boat. This is especially true of steep, rocky shores, where a large part of the sublittoral region consists of ledges and vertical or even overhanging rock faces, which would be quite inaccessible even if work from a small boat were attempted. In Sweden Gislén (1930), who employed a professional diver, has made an extensive general survey of the plant and animal associations characteristic of a rocky bottom in the Gullmar fiord. But for the British Isles previous knowledge relates only to the distribution of the larger and more conspicuous algæ (Cotton, 1912); although the flora of the German warships which were sunk in Scapa Flow has been investigated more closely by Miss Lyle (1929), also with the help of a professional diver.

In the summer of 1931, at the suggestion of Mr. G. A. Steven, of the Plymouth laboratory of the Marine Biological Association, the writers decided to test the possibility of carrying out a detailed investigation of this hitherto unexplored region by means of a diving helmet (see below). Such a helmet has been used by many workers in the tropics, but has not previously been tried in temperate waters, in view of certain supposed difficulties. Chief of these were :—

(i) Water too cold for an unprotected diver.
(ii) Poor visibility.
(iii) Excessive interference by rough weather.

These difficulties were found to be either not effective, or else easily surmountable, and are discussed in detail below.

(i) *Cold.* In July and August near Plymouth we found that we could each stay down for about a quarter of an hour at a stretch fairly comfortably, and at most for twenty minutes. We compensated ourselves for this shortness of time below water by working as a team generally of four people, of whom each went down in his turn; so that an hour's work could be done below water on any one day, and in favourable circumstances more. We found that the use of grease was of little help in combating the cold. Frequent diving led to a greatly increased appetite for sugar and treacle.

(ii) *Visibility.* There has always been plenty of light at the depths at which we have worked (down to six fathoms on the west coast of

Scotland). After rough weather the water was often turbid with silt in suspension, but even so with a sandy* bottom it was always possible to see clearly objects not more than two feet away.

(iii) *Rough weather.* On shores open to the English Channel the helmet could only be used with safety when the sea was moderately calm. A heavy "ground" swell makes diving impossible, even though the water is otherwise smooth, as it breaks with violence on the rocks. For this reason on an Atlantic coast diving would be difficult, but might be done from a boat. We were able to work under water on about half of the number of days during which operations were in progress, but in settled summer weather it should be possible to dive every day.

In this paper are presented the results of an ecological survey of a small area on the coast near Plymouth, extending from Low Water of Ordinary Spring Tides down to a depth of about 10 feet below this level. The survey was carried out between July 14th and August 14th, 1931, and between July 1st and August 3rd, 1932.

II. Apparatus and Methods.

As the methods employed were modified to suit conditions in our seas, a moderately full account of them is given below.

1. *The Diving Helmet and Pumps.*

The helmet which we used is similar to that described and figured by Beebe (1926), with the difference that, on the advice of Professor C. M. Yonge, in order to avoid "seeing double," we had only one window. Such a helmet fits loosely over the diver's shoulders, and the pressure of air inside it, which is maintained from above by means of pumps (see below), keeps the water out. A helmet of this type is comparatively light and easy to handle, and below water it restricts the movements of the diver very little. It is therefore suitable for use when working in crevices and on steep rock faces. Further, its use requires no previous experience, and the diver, who is in no way attached to it, can easily leave it and swim to the surface if anything goes wrong.

A steady supply of air was provided for the diver from two foot motor-tyre pumps, which were connected through Schræder valves to a T-piece; this last was connected through about 150 feet of garden hose with the helmet. One pump alone could in emergency supply sufficient air for the diver.

2. *The Telephone.*

A telephone system was installed, which enabled conversation to go on between the diver and those on shore. The system for speaking from the shore to the diver consisted of an ordinary microphone and ear-phone circuit. But since carbon granule microphones are liable to give trouble if they get damp, a different system was used for speaking in the reverse direction. The diver spoke into a high-resistance ear-phone, which was connected at the land end through a transformer to a one-valve amplifier. The output from this was fed into a pair of wireless headphones. In order to keep out the sea-water, the ear-piece and acting microphone were each nearly filled with paraffin wax and covered with a thin rubber toy balloon.

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* In a Scottish loch with a muddy bottom it was impossible to see at all once the mud was stirred up.

3. *Guide Ropes and Safety Lines.*

(i) In order to recover the helmet should the diver find it necessary to leave it and come to the surface, and in order to take the weight of the helmet off the diver's shoulders while he was entering or leaving the water, a rope was attached to the top of the helmet itself.

(ii) A rope, securely belayed to the rock at its shore end, and attached to a fairly heavy stone at its free end, was thrown out in the direction in which the diver was intending to go. On this the diver lowered himself and hauled himself up. It also assisted him in finding his way to the required spot, and enabled him to work against a rock wall, suspended at any depth.

(iii) A third rope was used for lowering collecting bags to the diver.

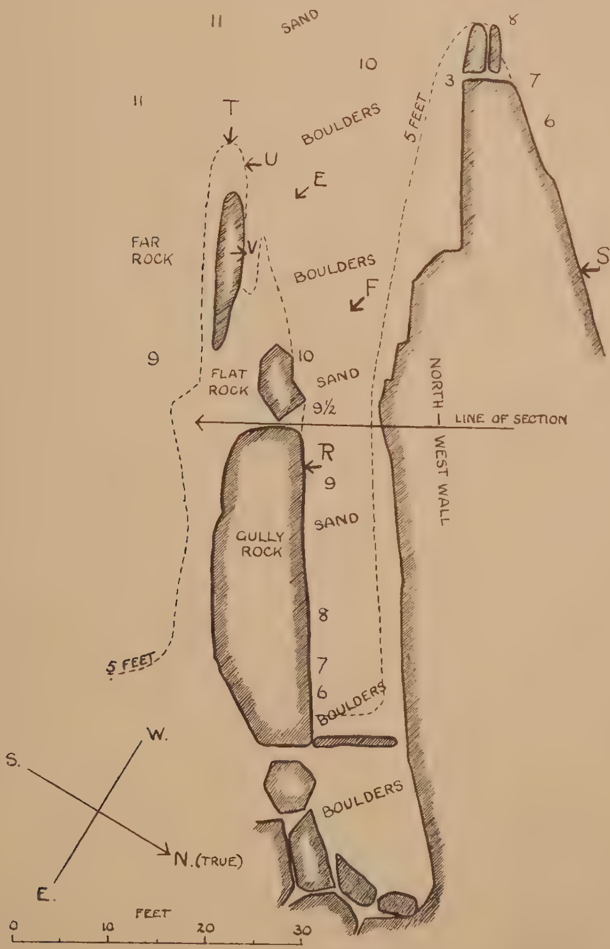
4. *Methods of Collecting.*

It seemed essential that data should be quantitative. Accordingly, (*a*) complete collections were made of all animals and plants from small selected areas of rock surface ; and (*b*) observations were made of the general distribution of those types of biological community of which the areas were considered typical. In 1931 (July 14th–August 14th) the selected areas were scraped clean with a strong knife into jars. This was a very slow process, and great care was needed to avoid loss of material. Therefore in 1932 (July) we used large bags with folding metal frames in the mouths. These frames were 1 foot × 1 foot or 2 feet × 1 foot, and when closed could be clipped together so as to keep the bags shut. Areas were scraped into these with a paint-scraper. With each of these methods there were some fast-moving animals (e.g. prawns, small fish) which must have escaped ; but as this work was directed mainly towards sedentary or slow-moving forms, which make up by far the greater part of the community, this does not matter much. Encrusting Coralline Algæ could seldom be scraped off the rock, and boring animals would not have been collected by this method, so that the collections must be considered incomplete in respect of these types. Although a standard size and shape of area would have been advantageous, we had in practice to take whatever areas were allowed by the configuration of the rock surface.

III. Description of Environment.

1. *Geographical Account.*

The locality chosen for a detailed survey by means of diving was in Wembury Bay, South Devon; and the work was done in the gully on the S.E. side of the reef next to and S.E. of "Tomb Rock" (Ordnance Survey. 1913). This gully runs approximately N.E. and S.W., and is formed in the Dartmouth Slates (Ussher, 1912). It has on its N.W. side a nearly smooth rock wall, which is at about 15-20° from the vertical,


11
SAND
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3
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BOULDERS
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U
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FAR ROCK
V
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F
9
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FLAT ROCK
SAND
NORTH
9½
LINE OF SECTION
WEST WALL
R
9
SAND
GULLY ROCK
8
7
6
BOULDERS
5 FEET
W.
S.
BOULDERS
N.(TRUE)
E.
FEET
0
10
20
30

Fig. 1.—Chart of the Gully.
All depths are marked in feet below chart datum.

facing upwards. On the S.E. side the rock surface is irregular and in most places overhanging (see section, Fig. 2). This gully is one of a series of similar parallel gullies which have been eroded in this particular way owing to the high angle of dip of the strata. The middle part of the gully (see Fig. 1) has a sandy bottom at a depth of 10 feet below the level of low water of ordinary spring tides. At the two ends of the gully the bottom is strewn with large boulders. At the S.W. end, beyond the boulders, the gully opens out to join the even sandy bottom which is characteristic of that part of Wembury Bay.

2. *Ecological Factors.*

The chief environmental influences which are likely to affect the flora and fauna of this gully are as follows :—

(i) *Slope of Surface.* This is believed to be of great biological importance (see p. 694), and has obvious connexions with illumination and with the settling of silt. It is shown in the section (Fig. 2).

(ii) *Light.* Measurements of the light intensity at various positions in the gully were made by Dr. Atkins by means of two cuprous oxide photoelectric cells. A full account of these cells, including the methods of use and the corrections to be applied, is given by Atkins and Poole (1933). While one cell remained exposed to the full light in air, the other was placed or held in any required position below water by the diver. The diver took precautions against shading his cell himself, and when it was in position he notified the shore party by telephone. Thus the illumination at any position was compared with that in air. A full table of the figures obtained is given in the Appendix. While such figures only represent the light intensity at one time of day and state of weather and tide, they may nevertheless be used as a basis for comparison. The chief feature is the very low percentage of light which reaches the bottom of the gully. This is due partly to shading by the gully walls, and partly to the opacity of the water, especially near the bottom. The lowest figure obtained—less than 1% of the intensity in air—was from a position in the Laminaria forest (see p. 685) at the base of the plants, below the "canopy" of fronds. In view of the shading by the gully walls, the absorption coefficient of the water remains uncertain, but in any case it must vary greatly, depending much on the roughness of the sea, and increasing downwards. The upper layers at high tide are probably comparatively clear. The biological significance of illumination in this gully is discussed later (see p. 694).

(iii) *Silt.* Both the presence of silt in the water, and the settling of silt, may be of importance. The amount of silt in the water was very variable, but was greater near the bottom. Sometimes the bottom foot of water was thick with seaweed remains. Silt carried along in the water by waves probably has a scouring action, especially near the bottom. The amount of silt which settles will depend partly on the slope of the rock surface, and partly on changes in the turbulence of the water.

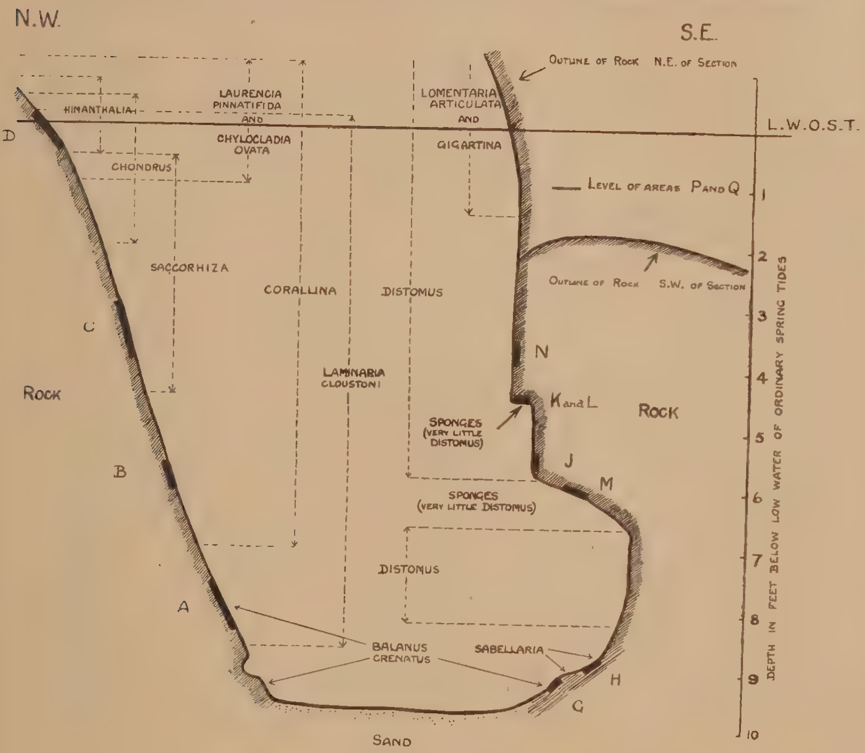
N.W.
S.E.
OUTLINE OF ROCK N.E. OF SECTION
L.W.O.S.T.
D
HIMANTHALIA
LAURENCIA PINNATIFIDA AND CHYLOCLADIA OVATA
LOMENTARIA ARTICULATA AND GIGARTINA
CHONDRUS
LEVEL OF AREAS P AND Q
SACCORHIZA
CORALLINA
DISTOMUS
OUTLINE OF ROCK S.W. OF SECTION
C
ROCK
N
LAMINARIA CLOUSTONI
K and L
ROCK
SPONGES (VERY LITTLE DISTOMUS)
J
B
M
SPONGES (VERY LITTLE DISTOMUS)
DISTOMUS
A
BALANUS CRENATUS
SABELLARIA
H
G
SAND
1
2
3
4
5
6
7
8
9
10
DEPTH IN FEET BELOW LOW WATER OF ORDINARY SPRING TIDES

FIG. 2.—Section of the Gully.

L.W.O.S.T. Low Water of Ordinary Spring Tides has been taken as equal in level with Chart Datum. This latter was estimated by comparisons of the level of the water in calm weather with the level predicted for Devonport.

L.W.E.S.T. Low Water of Equinoctial Spring Tides is variable in level, but is generally between a half and two feet below Chart Datum.

We hope in a future investigation to be able to obtain some comparative measurements of the turbulence in different parts of the gully.

(iv) *Wave action.* This part of Wembury Bay is exposed* to weather from S.W. by W. to S., and heavy storms occur in winter. It is possible that wave action is more intense on the N.W. wall than elsewhere, owing to the fact that waves rush up the intertidal slope above it, and then fall back with great force. It was observed during diving that the effects of a short choppy sea could scarcely be felt more than a few feet below the surface. But this part of the coast is much more subject to a comparatively long sea or swell, the influence of which extends to the bottom.

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* Some indication is given of the degree of exposure to wave action by the fact that in the intertidal region *Balanus balanoides*, *Chthamalus stellatus* and *Fucus vesiculosus evesiculosus* are present,—the last in small patches only, and poorly grown; while Pelvetia, *Fucus platycarpus* and Ascophyllum are absent. This combination is indicative of moderate exposure. It is hoped that later it may be possible, at any rate on some parts of the coast, to use certain common intertidal plants and animals as indicators of the degree of exposure to waves of a locality.

(v) *Exposure to the air.* This factor is not operative except in the intertidal region, which was studied in its lowest part only, merely for comparison with the contiguous infra-tidal region. Exposure to air may subject organisms both to desiccation and to rise in temperature.

(vi) *Variations in oxygen-content of the water, and other chemical factors.* These were not measured, as it is unlikely that areas in a region of so much water movement differ greatly in this respect. It is, however, possible that the fronds of the larger Algæ cause sufficient stagnation around their bases to produce an appreciable reduction in oxygen tension. It remains to be seen* to what extent the growth of various animals and plants upon the fronds and stipes of some of the larger algæ is to be ascribed to the presence of an environment more favourable than the rock surface itself (e.g. in oxygen tension, temperature, light, silt, turbulence), and to what extent it represents merely an overflow from the normal rock-surface community, induced by the struggle to gain a foothold.

(vii) *Temperature.* This rises near the surface on a calm warm day, but owing to unfavourable weather no adequate data were obtained. A discussion of this matter must therefore be withheld, although it is unlikely that temperature differences have any great significance.

IV. Distribution and Analysis of Types of Community.

There were two main associations in the gully, the "Laminaria forest association" (including the "Laminaria association" and the "Himanthalia association" of Cotton (1912)) and the "Distomus-Halichondria association." In this description only the most important species are mentioned; many others occurred and are given in the full lists in the appendix. The nomenclature followed is for algæ that used by Newton (1931), and for animals that given in the Plymouth Marine Fauna (Marine Biological Association, 1931), unless it is stated otherwise.

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* It is hoped to obtain data relating to this question during the course of a survey at present in progress on the W. coast of Scotland. A discussion of the influence of illumination on epiphytism is given by Børgesen (1908).

1. *The Laminaria Forest Association.*

This covered all the N.W. wall, and the boulders at the bottom of the gully. It occurred on all upward-facing rock surfaces in this and neighbouring gullies. When fully developed it consisted of :—

(*a*) A " canopy " layer formed by the fronds of one or more species of large brown alga (generally a Laminaria).
(*b*) An undergrowth of Corallina and other algæ.
(*c*) Species associated with the canopy.
(*d*) Species inhabiting the undergrowth and the holdfasts of the larger algæ.

(*a*) *The Canopy-forming Algæ.*

Himanthalia lorea was dominant in a narrow belt about a foot wide around the level of low water of ordinary spring tides. It occurred along the N.W. wall, on the E. side of " Gully " and " Far " rocks, and on the top of " Flat " rock (here above its more usual level). Corallina was present as a thick undergrowth. Himanthalia " buttons " were seen at lower levels, but never the reproductive parts. *Laminaria Cloustoni* was also present in this zone.

Saccorhiza bulbosa was dominant in 1931 in a belt just below the Himanthalia zone on the N.W. wall, and also on the boulders at the S.W. end of the gully. In 1932* it was almost completely absent from the gully except at the mouth, its place as dominant being taken by *Laminaria Cloustoni.*

Laminaria digitata was confined to the top of Far Rock (at L.W.E.S.T. level) and to ledges at L.W.E.S.T. level on the E. side of Far Rock and at the seaward end of the N.W. wall.

Laminaria saccharina was dominant in a small patch on the S.W. boulders in 1932.

Laminaria Cloustoni was dominant in all parts of the Laminaria forest association except for the above-mentioned places, and even in these (except for places occupied by *Laminaria digitata*) it was present. On the N.W. wall it was graded in size, being larger (up to 340 grams) near the top. Only small specimens (up to about 60 grams) were found near the bottom. On the boulders however it reached up to 280 grams or more ; and it was very large (up to 1800 grams) and covered with other growths (*Distomus variolosus* on the holdfast, *Rhodymenia palmata*, other red algæ and *Sertularia operculata* on the stipe) on the top of the narrow ridge N.W. of Far Rock.

Desmarestia aculeata and *Desmarestia ligulata* occurred fairly plentifully in 1931, but were scarce in 1932. The former was most common on the N.W. wall at about 5 feet from the bottom, while the latter was commoner above this level.

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* In 1933 (September) it was observed that *Saccorhiza bulbosa* had reappeared both on the boulders and on the N.W. wall.

(*b*) *The Undergrowth.*

Corallina spp. formed a dense growth all over the N.W. wall except at the bottom. (Upper limit, 1 foot above low water of ordinary spring tides and higher in cracks.) In places it was to some extent embedded in *Halichondria panicea.* From an examination of the samples collected, it appears that *C. squamata* predominated in the Himanthalia zone, but that lower down it was replaced by *C. officinalis.*

Chondrus crispus, *Chylocladia ovata*, and *Laurencia pinnatifida* were common in the zone of reproductive Himanthalia, and extended down to 1 or 2 feet below the bottom of this zone (see section). (Upper limit, 1 foot above L.W.O.S.T.) *Gigartina stellata* was locally plentiful in this zone.

Rhodymenia palmata was widely distributed (growing on the rock as well as on stipes of *Laminaria Cloustoni*).

Cladostephus verticillatus was locally abundant on the boulders.

(*c*) *The Population of the Canopy Layer.*

Rhodymenia palmata and *Sertularia operculata* grew on the stipes of the larger plants of *Laminaria Cloustoni.*

Obelia lucifera and *Gibbula cineraria* occurred on the fronds of some plants of *Laminaria Cloustoni.*

Patina pellucida (small* individuals only) occurred feeding on fronds and stipes of Laminaria spp., Saccorhiza, and Himanthalia.

Membranipora membranacea was nearly always present on fronds of *Laminaria digitata*, but only occasionally on those of *L. Cloustoni.*

(*d*) *The Population of the Undergrowth.*

Sessile forms (dealt with approximately in order from the rock outwards) included :—

An encrusting corralline alga forming a continuous coating over the tops of many of the boulders, and over the bottom of the N.W. wall. It may have extended upwards, but if so it was concealed by other growths.

Pomatoceros triqueter, widely distributed, and reaching as far as the upper limit of Corallina ; and *Umbonula verrucosa*, occasional. Both of these were fixed to the rock.

Balanus crenatus, at the bottom of both walls of the gully,—fixed to the rock.

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* Large individuals were occasionally found inside cavities, which they had no doubt themselves eaten out, in the holdfasts of large plants of *Laminaria Cloustoni.*

Hiatella arctica, at base of undergrowth and probably burrowing in the rock, but this was not observed.

Sabellaria spinulosa, occasional on the N.W. wall, but often filling the holdfasts of *Laminaria Cloustoni* growing on the boulders. On low horizontal ledges at the foot of the S.E. wall—ledges on which there were a few scattered and small plants of *Laminaria Cloustoni*—Sabellaria tubes formed a continuous coating to the rock.

Mytilus edulis (very small) and *Heteranomia squamula* on and among the undergrowth, but chiefly fixed to Laminaria holdfasts and Corallina.

Schizoporella hyalina, chiefly in small patches on holdfasts of *Laminaria Cloustoni*.

Membranipora pilosa, on holdfasts of *Laminaria Cloustoni* and on the fronds of red algæ.

The vegetative " buttons " of Himanthalia—which may be treated as part of the undergrowth—were always at least partly covered with Polyzoa (*Schizoporella hyalina* and *Membranipora pilosa*) on their undersides. On the other hand polyzoa and algæ were never found growing on the upper side of the " button," or on the fertile frond, of a healthy Himanthalia plant; although on one occasion a dead " button " was found to be covered all over with *Membranipora pilosa*.

Bunodactis verrucosa and *Spirorbis borealis* on Corallina.

Grantia compressa and *Sycon coronatum* attached to the undergrowth at random.

And motile forms :—

Nereis pelagica and *Platynereis dumerili*, the largest specimens being mostly inside holdfasts; and many other Polychæta errantia.

Jassa spp.

Elasmopus rapax.

Eurystheus maculatus (in areas " C " and " Z " this occurred in considerable numbers inside the holdfasts of *Saccorhiza bulbosa*); and many other Amphipoda.

Amphipholis squamata.

2. *The Distomus-Halichondria Association.*

This covered those parts of the S.E. wall which were overhanging, and all overhanging walls in a neighbouring gully. It ranged upwards above the level of L.W.O.S.T. in places. It consisted of :—

(*a*) A carpet-like growth of *Distomus variolosus* or of various sponges.
(*b*) Certain species (chiefly red algæ) projecting through (*a*) but with their bases embedded in it.
(*c*) Species living on or among the " carpet."
(*d*) Species associated with (*b*).

(*a*) Carpet-forming species.

Distomus variolosus was dominant on vertical or slightly overhanging rock faces. It formed in many places a continuous sheet. (Upper limit, about 2½ feet above L.W.O.S.T.)

Stolonica socialis was locally dominant at the seaward end of "Far Rock" in the region of transition from the Distomus-Halichondria association to the Laminaria forest association.

Sponges became more important the more the rock face overhung. On surfaces at an inclination of about 60° from the vertical, and facing downwards, sponges (especially *Halichondria panicea*, but also other species) were dominant, and Distomus was almost absent except where the inclined part adjoined a vertical Distomus-covered part.

(*b*) Projecting species.

Red algæ such as *Rhodymenia Palmetta*, *Cryptopleura ramosum*, and *Myriogramme Bonnemaisoni* were widespread below L.W.E.S.T. level on vertical or slightly overhanging surfaces, but they did not grow on the more steeply overhanging rock faces.

Gigartina stellata, *Laurencia pinnatifida*, and *Lomentaria articulata* were plentiful at and above the L.W.E.S.T. level, and in places grew thickly. (Upper limit 2½–3 feet above L.W.O.S.T.)

Hydroids, especially *Aglaophenia pluma* and *Sertularia operculata*, were common.

(*c*) The Population of the Sponge-Distomus "carpet."

Sessile species included :—various Cirripedia, *Umbonula verrucosa*, *Pomatoceros triqueter*—all growing on the rock surface, and generally much overgrown. *Pomatoceros triqueter* was very common at about 1 to 2 feet above L.W.O.S.T., under overhanging rocks, and near the upper limit of the carpet-forming species. The upper limit was 3 feet above L.W.O.S.T.

Hiatella arctica, *Sabella pavonina*, *Dasychone bombyx*, and other Polychæta sedentaria embedded in the sponges or Distomus.

Corynactis viridis, commonest under shelves in the sponge-covered areas.

Mytilus edulis.

Heteranomia squamula.

And motile species :—

Many Polychæta errantia, including *Nereis pelagica* and *Platynereis dumerili*.

Many Amphipoda, including Jassa spp., *Elasmopus rapax*, *Apherusa jurinei*, and various Caprellidæ.

Amphipholis squamata.

(*d*) The Population of the Projecting species included :—

Membranipora pilosa, growing in great profusion on red algæ, especially on *Gigartina stellata*.

Schizoporella hyalina, also very plentiful on red algæ, especially on *Rhodymenia Palmetta*.

Parajassa pelagica, nesting in the branches of *Sertularia operculata*.

Caprellidæ.

3. *Undergrowth Layers.*

More detailed examination of the undergrowth of the two sides of the gully leads to the subdivision of that of the Laminaria forest association into :—

(i) Outer undergrowth layer, consisting of larger undergrowth algæ such as *Rhodymenia palmata*, *Chondrus crispus*, etc., and generally rather loosely packed or sparse.

(ii) A middle layer of Corallina and holdfasts of Laminaria, which is dense.

(iii) A basal layer of species which are completely adherent to the rock surface, such as *Balanus crenatus*, *Pomatoceros triqueter*, and *Umbonula verrucosa*.

The "carpet" layer of the Distomus-Halichondria association corresponds with the middle layer of the Laminaria forest undergrowth, and it is this layer which harbours most of the animal species. The projecting species of the Distomus-Halichondria association correspond with the outer layer of the Laminaria forest undergrowth ; this layer is generally populated chiefly by Polyzoa, and is too loosely packed to give shelter to many motile animals. This detailed analysis is summarised in Table I.

TABLE I.

Layer.	Fully developed Laminaria forest association.	Distomus sub-association.	Halichondria sub-association.
Canopy	Present	None	None
Outer Undergrowth	Present	Present	Reduced
Middle Undergrowth	Present	Present	Present
Basal Undergrowth	Present	Present	Present

TABLE II.

ALL QUANTITIES HAVE BEEN REDUCED TO NUMBERS PER SQUARE FOOT.

Area.	Canopy Layer.	Undergrowth.	*Pomatoceros triqueter.*	*Umbonula verrucosa.*	*Balanus crenatus.*	*Bunodactis verrucosa.*	*Spirorbis borealis.*	*Nereis pelagica.*	*Platynereis dumerili.*	Other Polychæta errantia.	*Elasmopus rapax.*	*Eurystheus maculatus.*	Jassa spp.	*Caprella acanthifera.*	Other Amphipoda.	*Mytilus edulis.*	*Heteranomia squamula.*	Total No. of animal species in area.	Total No. of plant species in area.
D	Himanthalia (dominant). Some *Laminaria Cloustoni.*	Corallina, Chondrus, Laurencia, Chylocladia.	5	¾ to 1 sq. in.	0	54	49	11	0	10	3	0	2	0	2	216	16	26	8
C	Saccorhiza (dominant). Some *Laminaria Cloustoni.*	Corallina.	8	0	0	51	31	7	17	22	14	43	43	9	22	85	17	66	10
B	*Laminaria Cloustoni* (dominant).	Corallina (a little).	17	0	14	31	12	5	2	22	0	0	0	0	12	804	5	26*	4*
A	Very small plants of *Laminaria Cloustoni.*	Practically none (excluding holdfasts).	79	1 to 2 sq. ins.	872	0	0	12	2	5	0	0	5	2	6	265	17	30	4

* These values are probably too low, as area B is smaller than the other areas.

V. Analysis of Lists.

1. *Areas from Laminaria Forest Association.*

Areas A, B, C, D were taken from the N.W. wall. The basal part of the wall, from which Area A was collected, is very poorly illuminated (see Table VIII), and in the water around it there is much suspended matter, which probably has a scouring action. To one or both of these influences may be attributed the lack of undergrowth. The fauna of A differs from that of Areas B, C, D, which are higher up the wall, in the following respects (see Table II) :—

(i) Absence of *Spirorbis borealis* and *Bunodactis verrucosa*, which may be attributed to the absence of Corallina (or possibly to the presence of so much silt).

(ii) Abundance of *Balanus crenatus* and *Pomatoceros triqueter*, and

TABLE III.

Species Confined to or Characteristic of the Laminaria Forest Association.

- Algæ.
  - Desmarestia aculeata.
  - Desmarestia ligulata.
  - Cladostephus verticillatus.
  - Laminaria digitata.
  - Laminaria saccharina.
  - Laminaria Cloustoni
  - Saccorhiza bulbosa.
  - Himanthalia lorea.
  - Corallina officinalis.
  - Corallina squamata.
  - Chylocladia ovata.
- Cœlenterata.
  - †Obelia lucifera.
  - †Bunodactis verrucosa.
- Polychæta.
  - †Spirorbis borealis.
- Crustacea.
  - Anthura gracilis.
- Mollusca.
  - Paphia pullastra.
  - †Patina pellucida.
  - †Gibbula cineraria.
  - Tricolia pullus.
- And other rarer species.

TABLE IV.

Species Confined to or Characteristic of the Distomus-Halichondria Association.

- Algæ.
  - Myriogramme Bonnemaisoni.
  - Rhodymenia Palmetta.
  - Lomentaria articulata.
- Porifera.
  - Leucosolenia coriacea.
  - Leuconia nivea.
  - Leuconia gossei.
  - Amphilectus fucorum.
  - Myxilla rosacea.
  - Anchinoe fictitia.
- Cœlenterata.
  - Myriothela cocksi.
  - Dynamena pumila.
  - Sertularella polyzonias.
  - Sertularia operculata.
  - Plumularia setacea.
  - Aglaophenia pluma.
  - Corynactis viridis.
- Nemertini.
  - Œrstedia nigra.
- Polychæta.
  - Syllis prolifera.
  - Syllis variegata.
  - Eusyllis blomstrandi.
  - Sabella pavonina.
  - Dasychone bombyx.
- Crustacea.
  - Verruca strœmia.
  - Balanus perforatus.
  - Stenothöe marina.
  - Nototropis swammerdami.
  - Lembos websteri.
  - Caprella acutifrons.
  - Caprella tuberculata.
- Mollusca.
  - Kellia suborbicularis.
- Bryozoa.
  - Schizoporella linearis.
- Tunicata.
  - Distomus variolosus.
  - Amaroucium punctum.
  - Diplosoma listerianum.
- And other rarer species.

TABLE V.

SPECIES COMMON TO BOTH ASSOCIATIONS.

- Algæ.
  - Cryptopleura ramosum.
  - Laurencia pinnatifida.
  - Chondrus crispus.
  - Gigartina stellata.
- Porifera.
  - Sycon coronatum.
  - Grantia compressa.
  - Halichondria panicea.
- Polychæta.
  - Lepidonotus clava.
  - Eulalia viridis.
  - Eulalia sanguinea.
  - Syllis gracilis.
  - Trypanosyllis zebra.
  - Leptonereis glauca.
  - Nereis pelagica.
  - Platynereis dumerili.
  - Lysidice ninetta.
  - Sabellaria spinulosa.
  - Pomatoceros triqueter.
- Crustacea.
  - Balanus crenatus.
  - Janira maculosa.
  - Lysianassa ceratina.
  - Apherusa jurinei.
  - Apherusa bispinosa.
  - Gammarellus angulosus.
  - Elasmopus rapax.
  - Microdeutopus sp.
  - Eurystheus maculatus.
  - Jassa falcata.
  - Jassa dentex.
  - Parajassa pelagica.
  - Unciola crenatipalma.
  - Caprella acanthifera.
  - Porcellana longicornis.
- Pycnogonida.
  - Pycnogonum littorale.
  - Ammothea echinata.
- Mollusca.
  - Acanthochitona crinitus.
  - Heteranomia squamula.
  - Mytilus edulis.
  - Musculus marmoratus.
  - Hiatella arctica.
  - Rissoa parva.
- Bryozoa.
  - Membranipora pilosa.
  - Umbonula verrucosa.
  - Schizoporella hyalina.
- Echinodermata.
  - Ophiothrix fragilis.
  - Amphipholis squamata.
- Tunicata.
  - Aplidium pallidum.

presence of a considerable amount of *Umbonula verrucosa.* This is probably connected with the absence of undergrowth such as would cover them up. Area C, from the Saccorhiza zone, contains the largest number of animal species, and the largest numbers of individuals of most of the species.

Areas E, F, and Z were collected from the S.W. boulders, where the illumination is very poor under the Laminaria and Saccorhiza fronds (see Table VIII) and where there is at times a great amount of sediment and algal débris in the water. As in Area A, there is very little undergrowth, but Laminaria and Saccorhiza holdfasts, which function as undergrowth, are present. These areas are fairly poor in undergrowth inhabiting species, although the fauna is in most respects similar to that of B, C, D. The absence of *Balanus crenatus* is noticeable.

Areas G and H are from the base of the S.E. wall. Area G corresponds in position to some extent with Area A on the N.W. wall, and resembles it in its large number of *Balanus crenatus.* Area H, from a flat sandy ledge near the bottom of the S.E. wall, contains many individuals of *Sabellaria spinulosa.*

A list of species confined or nearly confined to the Laminaria forest association is given in Table III. The only five animals (marked with daggers) on this list which are common are associated especially with algæ peculiar to the association. It is not surprising that of the species common to both associations (Table V), all belong to the undergrowth.

2. *Areas from the Distomus-Halichondria Association.*

Areas R and S were collected about 1 foot above the level of L.W.O.S.T., and from their fauna it is clear that many species which are characteristic of the sub-littoral region extend upwards above the L.W.E.S.T. level on vertical or overhanging surfaces. These areas also contain several Tunicata which were not collected elsewhere. Apart from this a detailed study of the separate areas of this association does not reveal more than has already been noted in the preceding section from general observations.

Among the species confined to this association (see Table IV) the importance of Porifera, Cœlenterata, and Tunicata is remarkable,—and so in a lesser degree is that of Polychæta sedentaria, Cirripedia, and Caprellidæ.

3. *Transitional Areas.*

Areas T and U are to a large extent intermediate between the Laminaria forest and Distomus-Halichondria associations. Their fauna may be analysed as follows :—

TABLE VI.

	Species found in T and U.			T only.			U only.		
	C.	LF.	DH.	C.	LF.	DH.	C.	LF.	DH.
Algæ . . .	–	1	–	–	1	–	–	–	2
Porifera . . .	1	–	–	–	–	–	–	–	2
Cœlenterata . .	–	–	1	–	–	–	–	–	2
Polychæta . .	4	1	1	1	–	–	1	–	1
Crustacea . .	5	–	–	5	–	1	–	–	–
Mollusca . . .	2	–	–	1	2	–	–	–	–
Bryozoa . .	2	–	–	1	–	–	–	–	–
Echinodermata .	2	–		–	–	–	–	–	–
Tunicata . .	–	–	1*	–	–	–	–	–	–†
TOTAL . . .	16	2	3	8	3	1	1	0	7

* Also one species found nowhere else.
† Two species found nowhere else.
Column C=species common to both associations.
LF=species of the Laminaria forest group.
DH=species of the Distomus-Halichondria group.

Only species which occur in sufficient areas (i.e. at least two) and in sufficiently large quantities to be grouped in Tables III, IV and V have been considered in this analysis.

It will be seen that U shows a marked predominance of species from the Distomus-Halichondria association, as compared with T, which shows a less marked one of " Laminaria forest " species, and a great number of " common " species. A detailed study of the intermediate region might reveal an interesting transitional zonation, especially in the tunicates.

4. *New Records for Plymouth.*

Twelve animal species (see Table VII in the Appendix) were found which are not listed in the Plymouth Marine Fauna (Marine Biological

Association, 1931), and of these six are Porifera from the overhanging S.E. wall. This is explained by the fact that hitherto such localities have been very difficult of access.

VI. Discussion.

The differences between the various associations and sub-associations are so sharply marked, and show such close correlation with the differences in the external conditions of the habitat, as to suggest that the nature of these associations is rigorously controlled by environmental factors. The principal difference between the regions colonised by the two main associations is the slope of the rock surface, which will react on the fauna and flora in several ways, viz. :—

(i) *Ability of spores or larvæ to settle or develop.*

It is possible that some spores or larvæ may be unable to settle on overhanging rock surfaces, or that such positions may be unsuitable for their further development into adult organisms. The possibility that some such unknown factor excludes the larger brown algæ* from overhanging surfaces must not be ignored. The fact that the areas scraped clear in 1931 were almost all unrecognisable in 1932 shows that no such difficulty operates against the dominant members of the Distomus-Halichondria association, and that any given area continues to support a similar community even after such drastic interference. This was perhaps to be expected, since depopulation by storms must be a fairly frequent event.

(ii) *Settling of silt.*

It is noticeable that the most important of the species confined to the Distomus-Halichondria association are such as might be damaged by excessive deposition of silt. Unless they are excluded from the Laminaria forest association by competition or by some adverse effect of light, silt may be the responsible factor. It is possibly significant that whereas the stalked sponges were found plentifully on both walls of the gully, the encrusting species were confined to, or only flourished on the vertical or overhanging parts of the S.E. wall. The fact that hydroids were not found on the N.W. wall except on Laminaria fronds suggests that they may require to be held further off the rock face into a position where the water is more turbulent and silt-deposition less.

(iii) *Illumination.*

Laminaria Cloustoni occurred, though poorly and sparsely, on the Sabellaria ledge ; but on the upper part of the S.E. wall—a position which is better illuminated (see Table VIII)—it did not grow at all. While its poorness of growth on the former may possibly have been due to a deficiency of light, its absence from the latter cannot be attributed to this cause. Unless *Laminaria Cloustoni* is unable to gain a foothold among or compete with the members of the Distomus-Halichondria association, its absence from the upper part of the S.E. wall must in some way be connected with the slope of the surface. The grading in size of Laminaria plants on the N.W. wall may be due to the greater illumination near the surface; they probably often get torn off by storms, and the Laminaria forest would be regenerated more quickly where the illumination was greater. But there may also be some adverse factor such as silt in suspension affecting those near the bottom. The absence of *Saccorhiza bulbosa* in 1932 may probably be attributed to its being torn off by storms. The Sabellaria ledge at the bottom of the S.E. wall may be regarded as potential Laminaria forest which has failed to develop properly—possibly owing to inadequate illumination.

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* Intertidally Pelvetia and *Fucus platycarpus* are usually absent from overhanging rock surfaces.

Of the large brown algæ *Saccorhiza bulbosa* with its capacious holdfast supported by far the largest fauna, as regards both number of species and number of individuals; these included not only many small forms such as amphipods and polychætes, but also small fish and young echinoderms. *Laminaria Cloustoni* had a moderate fauna; but Desmarestia spp. and Himanthalia, which have small holdfasts, were in this respect unimportant.

The same types of community which are found below the low water of equinoctial spring tides reach a little way above this level, especially under ledges where there is protection from the adverse effects of being left high and dry. Colman (1933) has pointed out that at any time the belt of sea-shore which is within reach of the splashing of waves may be considered as being, for biological purposes, submerged. Thus infra-tidal conditions extend upwards above the level of L.W.E.S.T. by the width of the "splash zone." Many species found at this level may be regarded as really belonging to the infra-tidal region, and as having ranged upwards as far as conditions have allowed. Certain algæ, on the other hand (notably Himanthalia and Laurencia), belong properly to the lowest part of the inter-tidal region, and do not flourish below it. It is possible that illumination is the limiting factor. Strong evidence has been brought forward by Gail (1918) that insufficient illumination limits the downward distribution of Fucus in Puget Sound.

The part played by the basal undergrowth layer (encrusting Coralline algæ, barnacles, *Pomatoceros triqueter*, and *Umbonula verrucosa*) is especially interesting. The occurrence of barnacles both in the inter-tidal region and at the bottom of the N.W. and S.E. walls suggests that they are only able to live where they are free from competition with various other species. They are able to endure conditions which other species cannot endure, but in open competition become overgrown and smothered. The same is probably true to a less extent of other species of the basal undergrowth layer. Pomatoceros occurred most plentifully at the bottom of the N.W. wall and on vertical or overhanging faces in the lowest part of the inter-tidal region (up to 3 feet above L.W.O.S.T.), near the upper limit of the distribution of the main carpet-forming species. Unlike the barnacles, it is prevented, no doubt by the effects of exposure to air, from colonising the corresponding inter-tidal levels on the upward facing N.W. wall. From the occurrence of barnacle remains under *Distomus variolosus* and other carpet-forming species, and from an examination of the fauna of Area J(2),—an area which was scraped on the same site as the Area J(1) of the previous year—it seems that *Balanus crenatus* is (at any rate in some cases) an early coloniser of any available space, but that it later succumbs owing to competition. Our inability in 1932 to find any trace of the previous year's scrapings shows that recolonisation is very rapid.

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SUMMARY.

1. A diving helmet can be used successfully on British coasts.

2. An ecological survey, extending to a depth of 10 feet below low water of ordinary spring tides, has been made of a small area in Wembury Bay, S. Devon.

3. Below low water of ordinary spring tides upward facing rock surfaces were occupied by a "Laminaria forest association."

4. Below L.W.O.S.T. vertical or overhanging rock surfaces were occupied by a "Distomus-Halichondria association."

5. Large brown Algæ are excluded from the Distomus-Halichondria association by some factor connected with the slope of the rock surface, other than inadequate illumination.

6. Freedom from silt deposition may be responsible for many of the peculiarities of the Distomus-Halichondria association,—in particular for the importance of sponges, cœlenterates, and tunicates.

7. Barnacles play an important part in the recolonisation of bare rock surfaces.

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APPENDIX.

The following is a list of species recorded here for the first time at Plymouth :—

TABLE VII.

Porifera.	Examined by	Area of occurrence.
Leuconia nivea Grant [*Bowerbank*, 1874, 3, p. 11] .	M. Burton	K, L, M, U.
Leuconia gossei (Bowerbank) [*Bowerbank*, 1874, 3, p. 13]	M. Burton	M, S, U.
Ute glabra (Schmidt) [*Schmidt*, 1864, p. 23] . .	M. Burton	L.
Halichondria albescens (Bowerbank) (*Bowerbank*, 1874, 3, p. 265]	M. Burton	K.
Amphilectus fucorum (Johnston) [*Bowerbank*, 1874, 3, p. 142]	M. Burton	M, R,S.
Anchinoe fictitia (Bowerbank) [*Bowerbank*, 1874, 3, p. 265]	M. Burton	K, P, V.

POLYCHÆTA.	Examined by	Area of occurrence.
SYLLIS (EHLERSIA) FERRUGINA (Langerhans) [*Fauvel*, 1923, p. 269]	D. P. Wilson	E, K.
HETEROCIRRUS BIOCULATUS (Keferstein) [*Fauvel*, 1927, p. 96]	D. P. Wilson	J(1).
ISOPODA.		
HETEROTANAIS SP. ? ÖRSTEDI Kröyer [*Sars*, 1899, p. 14]	H. G. Jackson	U.
CYATHURA CARINATA (Kröyer) [*Barnard*, 1925, p. 140]	H. G. Jackson	S.
IDOTEA GRANULOSA Rathke [*Collinge*, 1917, p. 742]	H. G. Jackson	R.
AMPHIPODA.		
GAMMARELLUS ANGULOSUS (H. Rathke) [*Chevreux et Fage*, 1925, p. 204]	G. A. Steven	B, Q, T, S.

N.B.—Details concerning the areas of occurrence are given in Table IX.

MEASUREMENTS OF LIGHT INTENSITY.

The following measurements of light intensities were made on August 3rd, 1932, between 12 noon and 1 p.m., G.M.T., and the under-water values are expressed as percentages of the illumination in air. The illumination in air varied from 40·0 to 127 k.m.c. (thousands of metre-candles). In cases when the sun was shining an approximate correction $(\times \frac{\text{total light}}{\text{diffuse light}})$ has been applied, owing to the fact that the walls of the gully shaded the gully from direct sunlight. By means of this correction the under-water values are expressed as percentages of the diffuse light, and such corrected figures are shown in the table in brackets. The water was 12 feet deep when the measurements were made. The submarine photometer was held facing away from the rock, in such a way as to receive the maximum illumination.

TABLE VIII.

Position.	Illumination in air (k.m.c.).	Illumination in water (k.m.c).	$\frac{\text{Water}}{\text{Air.}}$
Just below surface	44·4	29·0	65%
N.W. wall, just below Himanthalia zone	40·9	8·10–15·2	20–37%
N.W. wall just below Himanthalia zone	50·0	10·8–18·9	22–38%
N.W. wall, bottom	122	1·36	1·1% (2·4%)
Middle of gully, 6ft. above bottom	127	15·2–18·3	12–14% (30%)
Middle of gully, 3 ft. above bottom	127	6·49	5·1% (12%)
S.E. wall, bottom	57·7	1·36	2·4%
S.E. wall, bottom	55·5	1·60	2·9%
S.E. wall, bottom	88·9	2·18	2·5% (3·9%)
S.E. wall, Sabellaria ledge (Area H)	57·7	1·40	2·4%
S.E. wall, Area J	40·0	1·49	3·7%
S.E. wall, Area K	39·7	0·65	1·6%
S.E. wall, Area N	38·5	3·24	8·4%
Ravine, Area V	38·9	1·60–3·77	4·1–9·7%
S.W. boulders, Laminaria forest, above fronds	40·8	2·18	5·3%
S.W. boulders, Laminaria forest, below fronds	42·2	0·27–0·44	0·64–1·0%

TABLE IX.

LIST OF SAMPLE AREAS.

Area.	Dimensions in inches.	Depth above (+) or below (−) L.W.O.S.T. in feet.	Slope of Surface.	Position.	Date of collection.
A	12 × 15	− 8	60–70° from horizontal, facing upwards	near bottom of N.W. wall	Aug. 3, 1931
B	6 × 10	− 6		on N.W. wall	Aug. 3, 1931
C	12 × 14	− 3½		on N.W. wall	Aug. 4, 1931
D	8 × 11	0		on N.W. wall	Aug. 7, 1931
E	Two separate squares each 12 × 12	− 10	horizontal	on S.W. boulders	July 16, 1932
F	15 × 15	− 10	horizontal	on S.W. boulders	July 18, 1932
G	4 × 4	− 9½	40°–50° from horizontal	at base of S.E. wall, in section	Aug. 12, 1931
H	6 × 10	− 9	nearly horizontal	on Sabellaria ledge, in section	Aug. 7, 1931
J(1)	6 × 9	− 5½	vertical	on S.E. wall, in section	Aug. 7, 1931
J(2)	4 × 4	− 5½	vertical	on same site as J(1)	July 18, 1932
K	5 × 14	− 4½	horizontal, facing downwards	on S E wall, in section	Aug. 9, 1931
L	2½ × 5	− 4½	horizontal, facing downwards	close to L	Aug. 9, 1931
M	6 × 20	− 6	overhanging, at about 40–50° from vertical	on S.E. wall, in section	July 18, 1932
N	5 × 9	− 3½ to − 4	vertical	on S.E. wall, in section	Aug. 13, 1931
P	9 × 8	− 1	vertical	at S.W. end of Gully Rock, in section	Aug. 13, 1931
Q	2½ × 4	− 1	vertical	close to P	Aug. 13, 1931
R	12 × 12	+ 1	vertical	on Gully Rock, facing N.W., in Gully	July 7, 1932
S	12 × 12	+ 1	overhanging at about 40–50° from vertical	in next gully, see chart	July 18, 1932
T	12 × 12	− 7	nearly vertical	at S.W. end of Far Rock	July 23, 1932
U	12 × 12	− 7	vertical	near S.W. end of Far Rock	July 16, 1932,
V	10 × 10	− 4	vertical	inside vertical cleft, about 3 feet wide, on N.W. side of Far Rock	Aug. 2, 1932
Z	–	− 10	horizontal	3 plants of Saccorhiza bulbosa, collected in a bag	Aug. 7, 1931

N.B.—The depths are taken to the middle of the Areas.

NOTES TO TABLES X AND XI.

In Tables X and XI the following abbreviations and signs have been used :—

fr. = fragment.
indiv. = individual.
s.q. = small quantity.
(?) identification not absolutely certain, owing to inadequacy of specimen.
(a) 13 of them very small.
(b) mostly *Corallina squamata*.
(c) quantity approximate.
(d) from holdfast of *Saccorhiza bulbosa*.
(e) on Corallina.
(f) +1 dead one.
(g) +2 dead ones.
(h) family inside *Verruca strœmia*.
(j) a few small colonies.
(k) degenerating.
(l) breeding.
(m) probably *Dendrodoa grossularia*.
(n) breeding in July, 1931.
(p) 1 ♀ was also found intertidally on Gully Rock.
(q) 38 of them from holdfast of *Saccorhiza bulbosa*.
(r) = 7 or 8 plants.
(s) small specimen or specimens.
(t) for nomenclature see Lebour (1933).
(u) *O.lucifera* includes *O. dichotoma* and *O. geniculata* in the Plymouth Marine Fauna.
(v) on *Gigartina stellata*.
(x) frond not collected.

The quantities of most Porifera have been estimated by volume (after preservation in alcohol). Rough plasticine models were made of the sponges, and the volumes of water displaced by the models were found. It is recognised that the sponges may have shrunk in the preservative.

TABLE X.

Areas from "Laminaria Forest" Association.

	Unit measured.	A	B	C	D	E	F	G	H	Z	Transitional Areas	
											T	U
Ectocarpus tomentosus	plant	–	–	–	–	1	–	–	–	–	–	–
Ectocarpus sp.	plant	–	–	–	–	–	1	–	–	–	–	–
Desmarestia aculeata . .		–	–	–	–	fr.	–	–	–	–	–	–
Desmarestia ligulata . .		–	–	–	–	fr.	–	–	–	–	–	–
Cladostephus verticillatus .	plant	–	2	–	–	–	–	–	–	–	–	–
Laminaria saccharina . .	plant	–	1 (s)	1	–	–	7	–	–	–	–	–
Laminaria Cloustoni . .	plant	7 (s)	5	4 (x)	2 (x)	22	5 (s)	–	–	–	–	–
Saccorhiza bulbosa . .	plant	–	–	1 (x)	–	1 (s)	–	–	–	3	–	–
Dictyota dichotoma . .	frond	–	–	–	–	–	1	–	–	–	–	–
Fucus serratus . . .	plant	–	–	1 (?)	–	–	1 (s)	–	–	–	–	–
Himanthalia lorea (fertile) .	plant	–	–	–	8	–	–	–	–	–	–	–
Himanthalia lorea (sterile) .	plant	–	–	5	7	–	–	–	–	–	–	–
Lithophyllum incrustans .	sq. ins.	–	–	½ (c)	2–3	–	–	–	–	–	–	–
Corallina officinalis . .	gram	–	5	}13	35 (b)	{1	–	–	–	–	9	2 (?)
Corallina squamata . .	gram	–	–			–	–	–	–	–	–	–
Delesseria sanguinea . .	frond	1 (s)	–	–	–	–	–	–	–	–	–	–
Membranoptera alata . .	plant	–	–	–	–	–	1	–	–	–	–	–
Myriogramme Bonnemaisoni		–	–	–	–	–	–	–	s.q.(s)(?)	–	–	fr.
Phycodrys rubens . .	frond	–	–	–	–	1	6	–	–	–	–	–
Polyneura Gmelini . .	frond	–	–	–	–	–	–	–	3 (?)	–	–	–
Cryptopleura ramosum . .	frond	–	–	4	–	–	–	–	2	–	8	3
Laurencia pinnatifida . .	frond	–	–	–	5	–	–	–	–	–	–	–

											Transitional Areas.	
	Unit measured.	A	B	C	D	E	F	G	H	Z	T	U
Polysiphonia nigrescens	plant	–	–	–	–	–	1	–	–	–	–	–
Heterosiphonia plumosa	plant	–	–	–	–	–	1	–	–	–	–	–
Ceramium rubrum	plant	1	–	–	–	–	–	–	2	–	–	–
Ceramium acanthonotum	tuft	–	–	1	6	–	–	–	–	–	–	–
Chondrus crispus	frond	–	–	–	5	–	–	–	–	–	–	–
Gigartina stellata	frond	–	–	–	–	–	2	–	–	–	–	–
Rhodymenia palmata	frond	–	–	–	–	1	–	–	–	–	–	–
? Rhodymenia	frond	6 (s)	–	–	–	1	3	–	s.q. (s)	–	–	–
Lomentaria articulata	gram	–	–	–	–	–	½	–	–	–	–	–
Chylocladia ovata	gram	–	–	–	2 (r)	–	–	–	–	–	–	–
Plocamium coccineum	plant	–	–	–	–	–	1	–	fr.	–	–	–
Sycon coronatum	indiv.	18	–	3	–	–	–	–	3	1	–	–
Grantia compressa	indiv.	6	–	6	5	–	–	–	3	–	–	–
Halichondria panicea	c.c.	–	5	10–12	½	–	–	–	–	–	14	4
Obelia lucifera (u)	colony	–	–	50 (c)	–	–	–	–	–	–	–	–
Aglaophenia pluma	plume	–	–	–	–	–	–	–	–	5	–	–
Bunodactis verrucosa (?)	indiv.	–	13	59	33	1 (?)	–	–	–	–	–	–
Zoantharia sp.	indiv.	–	–	–	–	–	–	–	1	–	–	–
Lepidonotus clava	indiv.	–	–	1	–	–	–		–	–	–	1
Harmothoe sp.	indiv.	1	–	1	–	–	–	–		–	1 (?)	1
Phyllodoce maculata	indiv.	–	–	1	–	–	–	–	–	–	–	–
Eulalia bilineata	indiv.	–	–	1	–	–	–	–	–	–	–	–
Eulalia viridis	indiv.	–	–	4	1	–	–	–	2	–	–	–
Eulalia tripunctata	indiv.	–	1	–	–	2	–	–	–	–	–	–
Eulalia punctifera	indiv.	–	–	–	–	–	–	–	1	–	–	–
Eulalia sanguinea	indiv.	–	–	2	–	–	–	–	1	–	–	–
Eulalia sp.	indiv.	–	4	2	2	–	–	1	–	–	–	–
Eteone picta	indiv.	–	-	–	–	–	–	–	1	1	–	–
Phyllodocid sp.	indiv.	2	1	3	–	–	-	–	–	-	–	–
Kefersteinia cirrata	indiv.	–	–	1	–	–	–	–	–	1	–	–
Syllis gracilis	indiv.	–	–	3	1	–	–	–	1	–	–	–
Syllis armillaris	indiv.	–	–	–	–	–	–	–	1	–	–	–
Syllis cornuta	indiv.	–	–	1	–	–	–	–	–	–	–	–
Syllis ferrugina	indiv.	–	–	–	–	1	–	–	–	–	–	–
Trypanosyllis zebra	indiv.	2	1	–	–	–	–	–	1	–	–	–
Syllid sp.	indiv.	–	–	1	1	–	–	–	1	–	–	1
Leptonereis glauca	indiv.	1	–	–	–	–	–	–	1	–	–	–
Nereis pelagica	indiv.	14	2	8	7	8	1	–	2	3	1	1
Platynereis dumerili	indiv.	2	1	15	–	4	–	–	9	5	5	3
Nereid sp.	indiv.	–	1	–	–	–	–	–	1	–	–	–
Eunice harassi	indiv.	–		2	–	–	–	–	–	–	–	–
Lysidice ninetta	indiv.	–	1	3	1	1	–	–	–	–	1	2
Eunicid sp.	indiv.	–	–	–	–	–	–	–	1	–	–	–
Dodecaceria concharum	indiv.	–	–	–	3	–	–	–	–	–	–	–
Sclerocheilus minutus	indiv.	–	–	–	–	–	–	–	1	–	–	–
Sabellaria spinulosa	indiv.	5	7	21	–	24	1	1	90	1	1	–
Amphitrite gracilis	indiv.	–	–	1	1	–	–	–	–	–	–	–
Polymnia nebulosa (s)	indiv.	–	–	1	–	–	–	–	–	–	–	–
Polymnia nesidensis (s)	indiv.	–	–	4	–	–	–	–	–	–	–	1
Nicolea venustula	indiv.	–	–	1	–	–	–	–	–	–	–	–
Polycirrus sp.	indiv.	1	–	1	–	–	–	–	1	–	–	–
Terebellid sp.	indiv.	–	–	fr.	–	–	–	—	fr.	–	–	–
Dasychone bombyx	indiv.	–	–		–	–	–	–	3	–	–	2
Pomatoceros triqueter	indiv.	99	7	9	3	6	–	–	3	1	1	1
Spirorbis borealis	indiv.	–	5 (e)	36 (e)	30 (e)	–	–	–	–	–	163 (e)	4 (e)
Balanus crenatus	indiv.	1009	6	–	–	–	–	56	–	–	13	–
Balanus balanoides	indiv.	–	–	–	5	–	–	–	–	–	–	–
Anthura gracilis	indiv.	2	–	3	–	–	–	–	–	–	–	–
Gnathia maxillaris	indiv.	–	–	1♀	–	–	–	–	–	–	–	–
Janira maculosa	indiv.	–	–	4	–	–	–	–	–	–	–	–
Lysianassa ceratina	indiv.	1	–	–	–	–	–	–	1	–	1	5
Apherusa jurinei	indiv.	–	–	1	–	–	–	–	–	–	5	–
Apherusa bispinosa	indiv.	1	–	1	–	–	8	–	–	–	14	–
Nototropis swammerdami	indiv.	–	–	–	–	–	–	–	–	2	2	–
Gammarellus angulosus	indiv.	–	2	–	–	–	–	–	–	–	1	–
Elasmopus rapax	indiv.	–	–	16	2	1	–	–	–	–	1	2
Hyale ? nilssoni	indiv.	–	1	–	–	–	–	–	–	–	–	–
Microdeutopus damnoniensis ♂	indiv.	1	–	–	–	–	–	–	–	–	1	–
Microdeutopus chelifer ♂	indiv.	1	–	5	–	–	–	–	–	1	–	–
Microdeutopus sp.	indiv.	2	1	8	–	–	–	1	1	–	–	1
Aorid sp.	indiv.	–	–	–	–	–	–	–	–	1♀	–	–
Photis longicaudata	indiv.	–	–	1	–	–	–	–	–	–	–	–
Eurystheus maculatus	indiv.	–	–	50 (q)	–	–	–	–	–	10	8	2
Amphithöe rubricata	indiv.	–	–	4	–	–	–	–	–	2	–	–
Jassa falcata ♂	indiv.	1	–	4	–	–	2	–	–	–	–	–
Jassa dentex ♂	indiv.	1	–	6	–	–	–	–	–	–	–	–
Jassa sp.	indiv.	4	–	40	1	1	13	–	4	–	3	–
Parajassa pelagica	indiv.	–	–	–	1	–	–	–	–	–	–	–
Unciola crenatipalma	indiv.	–	1	–	–	–	–	–	3	–	1	–

	Unit measured.	A	B	C	D	E	F	G	H	Z	Transitional Areas. T	Transitional Areas. U
Corophium bonelli	indiv.	–	–	–	–	–	–	–	2	–	–	–
Podocerus variegatus	indiv.	–	–	2	–	–	–	–	–	–	–	–
Caprella acanthifera	indiv.	2	–	10	–	–	–	–	1	2	12	1
Fragmentary Amphipoda	indiv.	2	–	10	–	–	–	–	1	5	–	–
Praunus inermis	indiv.	–	–	–	–	6	–	–	–	–	–	–
Fragmentary Mysidæ	indiv.	–	–	–	–	2	–	–	–	–	–	–
Porcellana longicornis	indiv.	–	–	1 (?)	–	1	–	–	–	–	–	–
Cancer pagurus	indiv.	–	–	–	–	–	–	–	–	3 (s)	–	–
Pilumnus hirtellus	indiv.	–	–	–	–	3	–	–	1	–	–	–
Pycnogonum littorale	indiv.	–	–	2	–	1	–	–	–	–	–	–
Nymphon gallicum	indiv.	–	–	–	–	–	1	–	–	–	–	–
Ammothea echinata	indiv.	2	1	–	–	–	–	1	–	–	–	–
Acanthochitona crinitus	indiv.	2	–	3	1	–	–	–	–	–	–	–
Heteranomia squamula	indiv.	21	2	15	10	9	–	–	6	–	15	22
Mytilus edulis (s)	indiv.	331	335	99	132	7	5	1	5	10	5	–
Musculus marmoratus	indiv.	1	–	3	–	–	–	–	–	–	1	7
Chlamys opercularis	indiv.	–	–	2 (s) (d)	–	–	–	–	–	–	–	–
Paphia pullastra	indiv.	–	–	2	2	5	–	–	–	2	–	–
Hiatella arctica	indiv.	–	5	10	8	–	–	–	2	–	–	–
Patella vulgata	indiv.	–	–	–	1	–	–	–	–	–	–	–
Patina pellucida	indiv.	–	–	3+	25	5	–	–	–	95	3	–
Gibbula cineraria	indiv.	–	–	–	–	1	2	–	–	8	–	–
Tricolia pullus	indiv.	–	–	1	–	1	–	–	–	–	2	–
Littorina littoralis	indiv.	–	–	–	–	–	–	–	3	–	–	–
Littorina ? rudis	indiv.	–	1 (s)	–	–	–	–	–	–	–	–	–
Rissoa parva	indiv.	1	1	7	1	2	–	–	–	1 (?)	–	–
Onoba candida	indiv.	–	–	–	–	1	–	–	–	–	–	–
Trivia sp.	indiv.	–	–	–	–	1	–	–	–	–	–	–
Nucella lapillus	indiv.	–	–	1	–	–	–	–	–	–	–	–
Nassarius incrassatus	indiv.	–	–	–	–	1	–	–	–	–	–	4
Retusa mammillata	indiv.	–	–	–	–	1	–	–	–	1	–	–
Membranipora pilosa	sq. ins.	–	–	<½	–	½	1	–	s.q.	½ (c)	4	–
Umbonula verrucosa	sq. ins.	1–2	–	–	⅓	s.q.	–	–	–	–	1–2	⅓
Schizoporella hyalina	sq. ins.	–	–	½ (c)	s.q.	1 (c)	½	–	s q	½ (c)	⅓	1(c)
Tubulipora lobulata		–	–	–	–	–	–	–	–	s.q.	–	–
Marthasterias glacialis	indiv.	–	–	1 (d) (s)	–	–	–	–	–	–	–	–
Ophiothrix fragilis	indiv.	–	1	7	–	7	4	–	–	6	6	11
Amphipholis squamata	indiv.	1	1	20	–	1	–	–	–	3	2	3
Cucumaria saxicola	indiv.	–	–	1 (d) (s)	–	–	–	–	–	–	–	–
Styelid sp.	zooid	–	2	–	–	–	–	–	–	–	–	–
Aplidium pallidum	colony	–	–	20–30 (e) (l)	–	–	–	–	–	–	–	–
Liparis sp.	indiv.	–	–	–	–	–	–	–	–	1 (d)	–	–

Transitional Areas (continued from above)

		T	U
Laminaria sp.	plant	2 (s)	–
Cystoclonoum purpureum	plant	1	–
Rhodymenia Palmetta	frond	–	3
Leuconia nivea	c c.	–	5
Leuconia gossei	c.c.	–	1–2
Halisarca dujardini	c.c.	–	1
Myriothela cocksi	indiv.	–	1
Sertularella polyzonias	colony	–	1
Corynactis viridis	indiv.	1	2
Harmothöe impar	indiv.	–	1
Lumbriconereis sp.	indiv.	–	1 (s)
Sabella pavonina	indiv.	1 (s)	2 (s)
Heterotanais ? örstedi	indiv.	–	1

		T	U
Synisoma lancifer	indiv.	1♂ (p)	–
Aora typica	indiv.	2	–
Plœnexes gammaroides	indiv.	1	–
Hippolyte varians	indiv.	2	–
Trivia arctica (t)	indiv.	–	1
Goniodoris nodosa	indiv.	2 (s)	1
Scrupocellaria reptans	colony	–	100 (c)
Bugula turbinata	colony	2	–
Polycarpa sp.	zooid	–	2
Styelid sp. ? Dendrodoa		–	s.q.
Stolonica socialis	zooid	55 (c)	200 (c)
Distomus variolosus	zooid	100 (c)	100 (c)

TABLE XI.

Areas from Distomus-Halichondria Association.

	Unit measured.	J (1)	J (2)	K	L	M	N	P	Q	R	S	V
Dictyota dichotoma .	frond	–	–	–	–	–	–	–	–	20 (c)(s)	2	–
Corallina officinalis .	gram	–	–	–	–	–	–	–	–	–	–	2 (?)
Corallina squamata .	gram	–	–	–	–	–	–	–	–	3	1	–
Nitophyllum punctatum	frond	–	–	–	–	–	–	–	–	–	–	3
Myriogramme Bonnemaisoni .	frond	–	–	–	–	–	–	–	–	–	5	3
Cryptopleura ramosum	frond	–	–	–	–	–	–	–	–	–	–	1
Laurencia pinnatifida .	frond	–	–	–	–	–	–	–	–	40 (c)	–	–
Pterosiphonia parasitica	plant	–	–	–	–	–	–	–	–	–	1	–
Brongniartella byssoides	plant	–	–	–	–	–	–	–	–	1	–	–
Heterosiphonia plumosa	plant	–	1	–	–	–	–	–	–	–	–	–
Halurus equisetifolius .	plant	–	–	–	–	–	–	–	1	–	–	–
Ceramium circinatum .	plant	–	–	–	–	–	–	s.q.	1	–	–	–
Ceramium echionotum .	plant	–	–	–	–	–	–	–	1	–	–	–
Chondrus crispus .	frond	–	–	–	–	–	–	12 (s)(?)	–	–	–	–
Gigartina stellata .	frond	–	–	–	–	–	–	5 (s)	50 (c)	1	–	–
Phyllophora epiphylla .	frond	–	–	–	–	–	–	–	–	–	–	12 (c)
Rhodymenia Palmetta	frond	16	–	–	–	–	9 (?)	–	–	–	–	3
? Rhodymenia . .	frond	–	5 (s)	–	–	–	–	–	–	–	–	–
Lomentaria articulata	gram	–	–	–	–	–	–	fr.	–	75 (c)	1	–
Plocamium coccineum .	plant	–	–	–	–	–	–	–	–	–	–	5
Leucosolenia coriacea .	c.c.	–	–	27	–	–	1	–	–	–	–	–
Sycon coronatum .	indiv.	–	–	–	–	1	–	–	–	–	–	–
Grantia compressa .	indiv.	2	2	3	4	15	–	7	–	–	1	14
Leuconia nivea . .	c.c.	–	–	3	3	5	–	–	–	–	–	–
Leuconia gossei . .	c.c.	–	–	–	–	½	–	–	–	–	½	–
Ute glabra . . .	c.c.	–	–	–	1	–	–	–	–	–	–	–
Halichondria panicea .	c.c.	11	–	–	10	150	–	1	–	9	40	½
Halichondria albescens	c.c.	–	–	2	–	–	–	–	–	–	–	–
Halichondria bowerbanki . .	c.c.	–	–	–	–	–	–	–	–	–	1	–
Hymeniacidon sanguinea . .	c.c.	–	–	–	–	–	–	–	–	4	5	–
Amphilectus fucorum .	c.c.	–	–	–	–	3	–	–	–	1	4	–
Myxilla incrustans .	c.c.	–	–	–	–	20	–	–	–	–	–	–
Myxilla rosacea . .	c.c.	–	–	–	–	2	25 (c)	–	–	–	–	–
Anchinöe fictitia .	c.c.	–	–	5	–	–	–	25 (c)	–	–	–	15
Chalina cinerea . .	c.c.	–	–	–	–	–	–	–	–	–	2	–
Myriothela cocksi .	indiv.	1	–	–	–	–	–	–	–	–	3	–
Dynamena pumila .	colony	–	–	–	–	–	–	–	–	20 (c)	–	25 (c)
Sertularella polyzonias	colony	–	–	–	4	8 (c)	–	–	1	–	–	1
Sertularia operculata .	colony	–	–	1	–	–	–	10	45 (c)	–	1	6
Kirchenpaueria pinnata	colony	–	–	–	–	–	–	–	18	–	–	–
Plumularia setacea .	colony	–	–	–	–	4	–	–	10 (c)	–	5 (c)	–
Aglaophenia pluma .	plume	1	–	40 (c)	1	–	24	250–300	–	1	–	–
Metridium ? senile .	indiv.	–	–	–	–	–	1 (?)	–	–	–	–	–
Corynactis viridis .	indiv.	5	–	26	15	38	15	–	–	–	–	7
Œrstedia dorsalis .	indiv.	–	–	–	–	–	–	–	–	–	–	3
Œrstedia nigra . .	indiv.	1	–	2	–	–	8	–	–	–	–	–
Lepidonotus clava .	indiv.	–	–	–	–	–	–	1	–	–	1	–
? Eunöe nodosa . .	indiv.	–	–	–	–	–	1 (s)	–	–	–	–	–
Harmothöe impar .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Harmothöe sp. . .	indiv.	–	–	–	2	3	2	–	–	1	1	–
Lagisca extenuata .	indiv.	–	–	–	–	–	–	–	–	–	–	1 (?) (s)
Eulalia viridis . .	indiv.	2	–	–	–	–	–	–	–	–	–	–
Eulalia sanguinea .	indiv.	1	–	2	1	2	–	–	–	–	1	–
Eulalia sp. . . .	indiv.	–	–	–	–	–	–	–	–	–	1	–
Syllis gracilis . .	indiv.	1	–	–	–	–	–	–	1	–	1	–
Syllis ferrugina . .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Syllis prolifera . .	indiv.	1	–	–	–	–	–	–	1	–	–	–
Syllis variegata . .	indiv.	4	–	–	1	–	–	–	–	–	–	–
Syllis armillaris . .	indiv.	–	1	2	–	–	4	–	–	–	–	–
Syllis sp. . . .	indiv.	–	1	–	–	1	–	–	–	–	–	–
Trypanosyllis zebra .	indiv.	2	–	1	2	1	1	2	–	–	1	–
Eusyllis blomstrandi .	indiv.	1	–	1	–	–	–	–	1	–	–	–
Grubea pusilla . .	indiv.	–	–	–	–	–	–	–	–	–	1	–
Autolytus pictus .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Autolytus sp. . .	indiv.	–	–	2	–	–	1	–	–	–	–	–
Syllid sp. . . .	indiv.	2	–	1	–	–	4	1	–	–	–	–
Leptonereis glauca .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Nereis pelagica . .	indiv.	2	–	5	1 (s)	7	5	2	–	1	11	5
Platynereis dumerili .	indiv.	11	1	–	–	5	1	–	1 (?)	–	16	10
Nereid sp. . . .	indiv.	–	–	–	–	–	1	–	–	2	1	2
Lysidice ninetta . .	indiv.	2	–	1	1	1	1	–	–	1	3	1
Eunicid sp. . .	indiv.	–	–	1	1	–	–	–	–	1	–	1 (?)
Heterocirrus bioculatus	indiv.	1	–	–	–	–	–	–	–	–	–	–
Arenicola sp. . .	indiv.	1 (s)	–	–	–	–	–	–	–	–	–	–
Sabellaria spinulosa .	indiv.	9	2	1 (?)	1	1	–	–	fr. (?)	1	–	1
Nicolea zostericola .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Sabella pavonina .	indiv.	2 (s)	–	3 (?) (s)	–	5 (s)	1 (s)	1 (?) (s)	–	–	38 (s)	–

	Unit measured.	J (1)	J (2)	K	L	M	N	P	Q	R	S	V
Potomilla reniformis	indiv.	1 (s)	–	–	–	–	1 (s)	–	–	–	–	–
Dasychone bombyx	indiv.	–	–	–	1	2	–	–	–	–	–	1
Fabricia sabella	indiv.	–	–	–	–	–	15	–	–	–	1	–
Sabellid sp.	indiv.	1	–	–	–	1	–	–	–	–	–	–
Pomatoceros triqueter	indiv.	6	1	–	–	7	2	2	4	11	46	–
Spirorbis borealis	indiv.	–	–	–	–	–	–	–	–	–	–	10 (e)
Verruca strœmia	indiv.	–	–	1	1	2	–	–	1	–	1	–
Balanus crenatus	indiv.	17	116 (s)	1	1	11	17	4	10+	15+	1	1
Balanus perforatus	indiv.	–	–	–	–	–	–	–	– (f)	2 (g)	1 (g)	–
Balanus improvisus	indiv.	–	–	–	–	–	–	–	–	1	–	–
Cypris larva	indiv.	–	–	–	–	1	–	–	–	–	–	–
Cyathura carinata	indiv.	–	–	–	–	–	–	–	–	–	1	–
Gnathia maxillaris	indiv.	–	–	–	–	–	–	–	–	–	(h)	–
Næsa bidentata	indiv.	–	–	–	–	–	–	–	–	1	–	–
Idotea granulosa	indiv.	–	–	–	–	–	–	–	–	6	–	–
Janira maculosa	indiv.	2	–	15	7	2	9	6	–	–	2	2
Lysianassa ceratina	indiv.	4	–	–	–	1	–	–	–	–	–	–
Leucothöe spinicarpa	indiv.	–	–	–	1	–	–	–	–	–	–	–
Stenothöe marina	iodiv.	–	–	–	1	–	–	1	–	–	4	–
Apherusa jurinei	indiv.	–	–	–	–	–	3	8	2	11	16	–
Apherusa bispinosa	indiv.	–	1	1	–	1	–	–	–	–	–	2
Nototropis swammerdami	indiv.	–	–	1	–	1	1	–	–	–	–	–
Gammarellus angulosus	indiv.	–	–	–	–	–	–	–	4	–	5	–
Elasmopus rapax	indiv.	5	–	6	2	1	1	6	–	–	5	1
Microdeutopus sp.	indiv.	–	–	–	5	2	1	–	–	–	–	3
Lembos websteri	indiv.	1	–	1	1	1	–	–	–	–	–	2
Eurystheus maculatus	indiv.	1	–	–	3	1	–	–	–	–	–	3
Jassa falcata ♂	indiv.	–	–	–	–	–	2	–	1	–	3	–
Jassa dentex ♂	indiv.	–	–	–	1	–	–	–	–	–	–	–
Jassa sp.	indiv.	4	–	46	–	1	57	3	4	2	16	1
Parajassa pelagica	indiv.	1	–	93	–	–	1	83	142	3	–	–
Unciola crenatipalma	indiv.	–	–	2	–	–	1	–	–	–	–	–
Corophium bonelli	indiv.	–	–	1	–	–	–	–	–	–	–	1
Podocerus variegatus	indiv.	–	–	–	–	–	–	–	1	–	–	–
Pseudoprotella phasma	indiv.	–	–	–	–	–	1	–	–	–	–	–
Caprella acanthifera	indiv.	–	–	2	–	–	5	–	–	–	1	2
Caprella acutifrons	indiv.	–	–	–	–	–	9	7	1	1	–	–
Caprella tuberculata	indiv.	–	–	61	4	–	4	–	–	–	–	–
Fragmentary Amphipoda	indiv.	–	–	12	–	2	1	5	–	–	–	1
Hippolyte varians	indiv.	–	–	–	–	–	–	–	–	–	–	2
Porcellana longicornis	indiv.	–	–	–	–	–	–	–	–	–	–	1
Cancer pagurus	indiv.	–	–	–	–	–	–	–	–	–	1 (s)	–
Pycnogonum littorale	indiv.	–	–	–	–	–	–	–	–	–	1	–
Ammothea echinata	indiv.	–	–	–	–	–	–	1	–	–	–	–
Acanthochitona crinitus	indiv.	–	1	–	–	1	1	1	–	2	2	1
Heteranomia squamula	indiv.	16	13	10	7	20	1	7	–	3	1	5
Mytilus edulis (s)	indiv.	–	–	2	–	1	1	12	25	39	65	–
Musculus marmoratus	indiv.	4	1	3	–	1	–	–	–	–	3	5
Kellia suborbicularis	indiv.	1	–	1	2	–	–	–	–	–	–	–
Hiatella arctica	indiv.	4	–	1	1	–	1	–	–	3	10	–
Patina pellucida	indiv.	–	–	–	–	–	–	–	4	–	–	–
Calliostoma zizyphinum	indiv.	–	–	–	–	–	–	–	–	–	–	1
Littorina littoralis	indiv.	–	–	1	–	–	–	–	–	–	–	–
Littorina sp.	indiv.	–	–	–	–	–	–	–	–	–	–	1 (s)
Rissoa parva	indiv.	1	–	–	–	–	–	1	–	–	–	–
Lamellaria perspicua	indiv.	–	–	–	–	1	–	–	–	–	–	–
Nassarius incrassatus	indiv.	–	–	–	–	–	–	–	–	–	–	1
Polycera quadrilineata	indiv.	–	–	–	–	–	–	–	1	–	–	–
Scrupocellaria reptans	colony	1	(j)	–	–	–	–	–	–	–	–	–
Bugula turbinata	colony	–	–	–	–	2	–	–	–	–	–	–
Membranipora pilosa	sq. ins.	s.q.	–	–	–	s.q.	–	1–2 (v)	3½–4 (v)	s.q.	½	3
Umbonula verrucosa	sq. ins.	–	–	s.q.	–	s.q.	–	–	–	7 (c)	4	–
Schizoporella hyalina	sq. ins.	8–9	s.q.	–	–	–	25 (c)	–	–	s.q.	s.q.	2
Schizoporella linearis		s.q.	–	–	s.q.	s.q.	–	–	–	–	–	–
Alcyonidium hirsutum		–	–	–	–	–	–	–	–	s.q.	–	–
Ophiothrix fragilis	indiv.	1	–	1	1	2	1	1	–	–	–	1
Amphipholis squamata	indiv.	–	–	–	–	–	–	–	–	–	1	–
Dendrodoa grossularia	zooid	–	–	–	–	–	–	–	–	–	1	–
Distomus variolosus (n)	zooid	850–1000	10	–	–	200 (c)	400–500	1500 (c)	80–100	200 (c)	1500–2000	600–700
Styelid sp.		–	–	–	–	–	–	–	–	–	s.q. (s)	–
Sidnyum turbinatum	colony	–	–	–	–	–	–	–	–	1 (s) (l)	–	–
Amaroucium punctum		–	–	–	–	–	–	–	–	s.q.	s.q. (l)	–
Amaroucium nordmanni	colony	–	–	–	–	–	–	–	–	2	–	–
Aplidium pallidum	colony	–	–	–	–	1 (s) (l)	–	–	–	s.q. (l)	2 (l)	–
Morchellium argus	colony	–	–	–	–	–	–	–	–	–	1 (s)	–
Diplosoma listerianum	sq. ins.	–	–	2–3 (l)	–	–	1	–	–	s.q.	s.q.	–
Trididemnum tenerum		–	–	–	–	–	–	–	–	–	s.q. (l)	–
Didemnid sp.		–	–	–	–	–	–	–	–	–	s.q. (k) (l)	–

Studies on *Stylonethes sterkii* sp. nov. I. Morphology and Systematic Position.

By

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With Plates I and II, and 1 Text-figure.

While studying some of the ciliates found in the region of the Marine Biological Laboratory at Plymouth, England, from January to May, 1929, the author collected from Chelson Meadow a hypotrich which undergoes binary fission only during encystment. This interesting behaviour, which appears to be rare among the Hypotrichida, led to a study of the morphology of the free-swimming form, preliminary to further investigations, including a study of both protective and reproductive cysts.

The organism has been named *Stylonethes sterkii*, reasons for which are presented in this paper.

Acknowledgment.

This investigation was begun when the author was a Fellow of the Oregon Division of the American Association of University Women, in the year 1928–29. She wishes to extend thanks to Dr. E. J. Allen, F.R.S., Director of the Marine Biological Laboratory of the United Kingdom, Plymouth, England, for the use of a table and for the collecting assistance and equipment put at her disposal during her stay at the laboratory; to Dr. Harold Kirby, Jr., of the University of California at Berkeley, for criticizing the manuscript; and to Dr. C. V. Taylor of Stanford University, for his many kindnesses and helpful suggestions. The writer is also indebted to Dr. C. A. Kofoid of the University of California, for the use of his extensive library.

TECHNIQUE.

Culture.

Both protective and reproductive cysts of *S. sterkii* remain viable when dried. This discovery made possible a transfer of the new hypotrich in May, 1929, from Plymouth to Stanford University, where the strain has been continued to the present time (July, 1933).

The following wheat infusion method of culturing was used exclusively. Twenty grains of wheat were cracked and then boiled in 15 c.c. of glass distilled water for from three to five minutes. The fluid containing numerous starch grains was used immediately after cooling and was transferred to the culture by means of a pipette having a bore of 1·5 mm.

Experiments have shown that thriving cultures are most easily maintained when complete evaporation of the medium takes place at intervals. Consequently, the organisms were grown in watchglasses holding conveniently about 4 c.c. of fluid. These were ordinarily enclosed in Petri dishes to prevent evaporation and to facilitate handling, but when mass encystment and complete evaporation of the medium was desired, the cover was removed. Or, the cover may be partly removed so that it protects the watchglass from dust but leaves a wide open gap between the two dishes. Within 8–10 hours, at a temperature varying from 15–22° C., the cultures were completely dried out.

New cultures were started daily when free-swimming individuals were wanted for study. By means of a mouth pipette twenty organisms from a thriving culture were transferred to a watchglass containing 4 c.c. of tap water and a drop of fresh wheat infusion. A drop of infusion was added daily to old cultures until protective cysts began to appear (2–4 days). Then they were allowed to dry out. Thus it can be arranged that there are always on hand about as many new cultures as old ones, and a reserve supply of dry cysts. If the study of active organisms is to be suspended for a few days or weeks, it is safe to rely upon the stock of dry cysts to begin new cultures, as was proved by the transfer of cysts in watchglasses from England to California. These cysts were about three weeks old when they arrived. Excystment occurred in three to four hours after distilled or tap water had been added.

Methods of Preparation.

The following description of *S. sterkii* is based mainly on observations made upon the living organism, although for purposes of confirmation and for study of fine details of structure, permanent mounts were made. The iron-alum-hæmatoxylin method of staining was most frequently used, after killing and fixing in Bouin's or Schaudinn's fluid (without acetic acid), the latter being better for the free-swimming forms, and the former for the cysts. Bresslau's (1921) China blue relief staining method was found to be excellent for a comparative study of external structures.

It is a difficult task to observe this form under the high powers of the microscope in living condition for the two following reasons: Rapid evaporation of the medium bursts the pellicle very easily, and the organisms encyst if evaporation proceeds slowly. However, with patience it is possible to acquire skill in manipulation whereby the living organism may be observed for two hours, or even longer in some cases. The locomotor organelles sooner or later stop beating, and after a quiescent period they sometimes function again just before death and disintegration. A minute drop of 10% alcohol, added to the hanging drop by means of a fine pipette, retards the movement of the organisms within a shorter time, and if evaporation is gradual the protoplasm eventually coagulates without much distortion, so that even after death the structures stand out quite clearly. A 1% solution of eurythane was also tried with some success.

General Morphology.

The body form of *Stylonethes sterkii* (Plate I, Fig. 1) may in general be described as an elongated ellipsoid, with a shallow excavation in the anterior portion of the left side. The ventral surface is slightly concave, the periphery is rounded, and the dorsal surface is broadly arched, the body being thickest centrally.

A thin and elastic pellicle, however, permits considerable modification in form. Especially is this apparent when the animal is gorged with food. The dorsal surface is then highly arched, and the anterior end is smaller than the broadly rounded posterior end. Individuals containing few food vacuoles sometimes are bluntly pointed posteriorly.

The structure of the anterior extremity is extraordinarily complex. Ventrally it terminates in a narrow and inconspicuous projecting lip of uniform width. Dorsally it gives rise to a series of typical membranelles, which extend from the anterior end of the right median ventral row of cirri (described below) to the extreme left side of the body, where they pass ventrally and posteriorly to form the left border of the peristome.

The longest membranelles are found at the most anterior point of the body, and they become shorter gradually away from this point in either direction. The bases of the first twelve or thirteen membranelles, beginning at the right, slope downward on the lip. The turn to the ventral surface is accomplished by the next six or seven membranelles, and posterior to these the bases slope gently downward from the margin of the peristome toward the periphery of the body. The peristomal membranelles gradually come to point ventrally and finally they project toward the midline. The number of membranelles varies. From 25 to 48 have been counted, the number being smaller in small individuals, and larger in large individuals.

Thus far the membranelle region is essentially the same as that described in many other members of the Hypotrichida, such as *Holosticha rubra* Ehrenberg (Wallengren, 1900) and *Euplotes patella* Ehrenberg (Taylor, 1929). However, in *S. sterkii* additional and unique structures are situated between the bases of the membranelles.

In the first place, small elevations, within which are found deeply staining spherules, arise in these narrow spaces (Plate II, Fig. 2). The spherules are most conspicuous in the first seven or eight inter-membranellar spaces, beginning at the right, and in size (largest about ·6μ) form a closely graded series so that the tenth or eleventh is barely visible. Beyond this point none can be seen, and if present they must be exceedingly small. Careful focusing from the dorsal surface or a frontal view reveals the fact that the first seven or eight spherules are double. The remainder appear to be single. Considerable variation in respect to number was noted. A small individual may have as few as eight. However, without exception, these spherules are clearly evident in organisms killed in Schaudinn's fluid (without acetic acid) and stained with Heidenhain's hæmatoxylin. This is true even when the preparation is greatly de-stained, thus showing exceedingly strong affinity for the dye. They were seen also in the living state as rounded bodies of greater density than that of the surrounding cytoplasm. The function of these unusual structures is not known.

Interpolated between the right side of each membranelle (except the first) and the left side of the elevation is a small, slender motile structure, which at rest is directed at an angle toward the apposing membranelle; that is, in a direction away from the peristome. Its base is about two-thirds the length of the membranelle base and so inserted that both proximal and distal ends of the membranelle base extend beyond it. This observation is most easily made in China blue preparations and in those individuals which have rounded up so that the frontal surface is uppermost. The length of this small organelle measures about 3·5 microns in living condition. As observed in China blue preparations, it was found

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EXPLANATION OF PLATES.

All figures were drawn with the aid of the camera-lucida.

PLATE I.

Fig. 1.—*Stylonethes sterkii* sp. nov., ventral aspect. Semidiagrammatic drawing of living organism. × 800.

PLATE II.

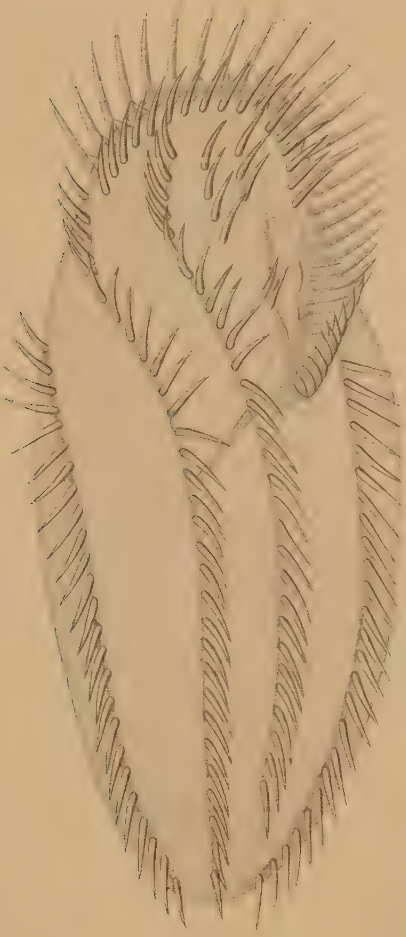
Fig. 2.—Anterior extremity, dorsal view, showing position of membranelles, inter-membranelles, and spherules within elevations. Semidiagrammatic. Heidenhain's hæmatoxylin stain. × 1896.

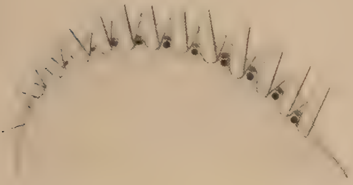
Fig. 3.—Right end of membranelle series. Membranelles, inter-membranelles, and cirri of transverse row are fimbriated. Light line between membranelles and cirri indicates lip, which was flattened in preparation. China blue relief stain. × 1290.

Fig. 4.—Dorsal aspect, showing three longitudinal rows of cilia. Living organism. × 750.

Fig. 5.—Note accumulation of granules at anterior end. Dorsal view. Heidenhain's hæmatoxylin stain. × 750.

Fig. 6.—Macronuclei and micronuclei, ventral view. Heidenhain's hæmatoxylin stain. × 750.





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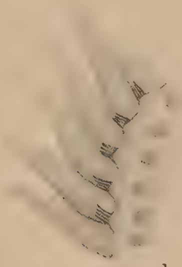

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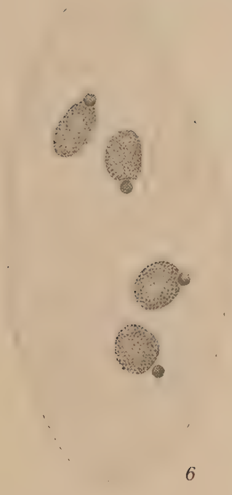

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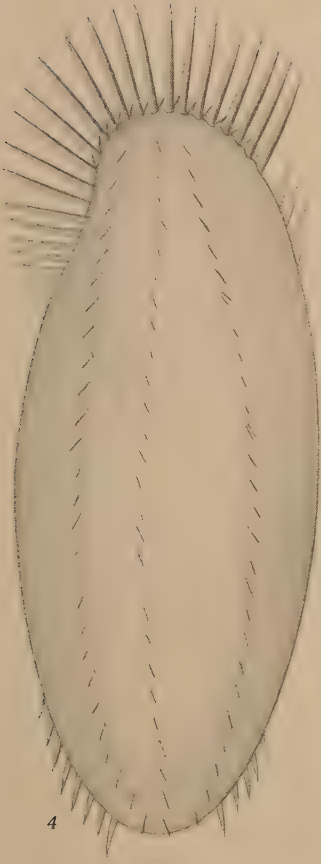

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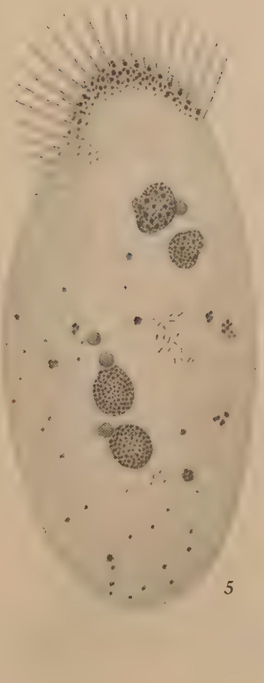


5

to be composed of cilia, similar to cirri, membranelles, and undulating membranes, since it shows fimbriation (Plate II, Fig. 3) when cirri and membranelles in the same specimen are thus separated into their component parts.

These minute inter-membranelles were first seen in the living organism and it was thought that their movement might be a passive one caused by the pressure of the two membranelles upon them, first on the one side and then on the other. This is not the case, however, for when observing an organism in a hanging drop preparation just prior to death due to the evaporation of the water, the larger motile organs, such as the membranelles, may cease movement, while these smaller structures continue vigorous movement. It sometimes happens that both stop functioning at the same time, or, the smaller structures may stop first, but occasions such as described above often occurred. Whether or not these organelles are present between all the membranelles is not known. The largest number counted was found in an individual having 38 membranelles. Beginning at the right, fourteen intermembranelles were clearly evident, and if they are present between the remaining membranelles, they must be very small.

While looking through the literature for recently described genera of the Hypotrichida, the writer encountered the article of von Gelei (1929) in which he briefly described " Nebenmembranellen " or " Zwergmembranellen " in *Spirofilum tisiæ* n. sp., n. gen. (according to Rossolimo (1929), a new species of the genus Hypotrichidium Ilowaisky, 1921). The position of this organelle, according to von Gelei, seems to be similar to that just described for *S. sterkii*, i.e. between the membranelles, but whether or not the structure is the same cannot be determined from the information given. Ilowaisky (Rossolimo, 1929) studied only the living specimens of his new form, *H. conicum*, and did not mention having seen minute organelles between the membranelles. Von Gelei's description (1929, p. 175) is as follows :—

" Mir ist an diesen Membranellen eine merkwürdige Erscheinung aufgefallen, die nämlich, dass neben beiden Organen an ihrer einander zugekehrten Seite noch eine weitere kleine Nebenmembranelle entwickelt ist. . . . Die Höhe dieser Zwergmembranellen ist gering, aber doch variabel ; einmal habe ich in einem Fall mit der regelrechten eine gleich grosse beobachtet. Der Bau und die Bedeutung dieser Nebenmembranellen ist mir unbekannt. Ihre Bewegung wurde auch nicht beobachtet, nur aus der Querschnittsform erschlossen."

Four longitudinal, uninterrupted rows of closely set cirri constitute the most conspicuous feature of the ventral surface. Two are median in position and two are lateral. The median rows are longer than the laterals, extending across the frontal field with a shallow curve to the right. The right lateral row originates at the periphery about one-third of the way back from the anterior end, and from this point posteriorly it becomes set in from the margin, as shown in Plate I, Figure 1. The anterior origin of the left lateral row is posterior to the peristome, about 8·5 microns from the body periphery. With the exception of the left median row, in which about four or five of the most posterior cirri are constantly missing, all the longitudinal rows extend almost to the posterior extremity of the body (Plate I, Fig. 1). Each row is set within a distinct groove in the pellicle, which is most clearly seen at the anterior end of the right lateral row. This groove extends over the rounded periphery to terminate on the margin of the dorsal surface. In individuals with few food vacuoles the longitudinal rows are equidistant from each other, but with increase in food contents, the median rows are slightly closer to each other than they are to the laterals.

The cirri in the longitudinal rows are more closely approximated to each other in some individuals than in others, and the number in each row in different individuals varies. Counts can be made on living specimens, but they can be easily and more carefully made on animals stained with China blue. However, in these preparations only in rare instances are all the four rows visible for their entire length, due to the contraction of the posterior extremity. (See summary below.)

On the ventral surface, posterior in position to the membranelle series, is a semicircular row consisting of a variable number of cirri. The position of the first cirrus at the right is constant—posterior to the first membranelle and opposite the first cirrus of the right median longitudinal row of cirri. Since the spaces between these cirri tend to be equal, the location of the last cirrus and the length of the row depends upon the number of cirri present in this row, which may be from 12 to 22. This interesting departure from the ciliation ordinarily found in the Hypotrichida has also been described by Penard (1922) in *Keronopsis helluo*, and recently by Kahl (1932) in the two species of his new genus Paraholosticha. According to the former investigator, the transverse row extends only about half-way across the anterior end.

Additional frontal cirri are disposed in two short rows to the left of the left median longitudinal row of cirri, the spaces between the three rows being approximately equal to each other. Immediately to the left is the peristomal groove. The number of cirri is variable within each row. From two to six have been found in the right row and from one to five, in the left row ; the smallest number in any one individual is three, and the largest number, ten.

The variation in number of frontal cirri does not indicate that there are races or strains within the species having a constant pattern of frontal cirri. Pure line cultures have been grown and these show all the variations of the frontal cirri pattern found in a mixed culture. The two daughters of a single individual may vary in respect to the number of frontal cirri.

Isolated cirri originate at the right peristomal border posterior to the frontals. Their number varies from one to three.

The following is a summary of cirri counts made upon five living, unstained individuals, together with the number of membranelles and the length of the organism.

	Body Length.	Membr.	Trans. Row.	Frontals R., L.		Isol.	Longit. Rows R. to L.
1.	100μ	29	14	3	1	1	23, 29, 23, 20
2.	108	34	15	3	2	1	20, 24, 25, 20
3.	145	48	20	5	4	3	27, 38, 38, 30
4.	148	38	17	4	3	3	29, 32, 29, 27
5.	152	38	18	4	2	2	26, 32, 30, 25

There is no appreciable difference in size among the ventral cirri. Except for the first two or three cirri at the anterior end of the right lateral and right median rows, and the isolated cirri, which appear to be slightly smaller, there is a remarkable uniformity in size of all the cirri of an individual. But the size of the cirri in different individuals varies, as is to be expected. The largest found measured fourteen microns in length.

Three longitudinal rows of cilia are found on the dorsal surface (Plate II, Fig. 4). The cilia are about three microns in length and are placed about five to six microns apart. Frequently two cilia originate at the same point. The dorsal cilia are not immotile (or very slightly movable) spines or bristles as found in *Euplotes worcesteri* Griffin (1910) and many other hypotrichs, but are definitely motile cilia, as can be readily demonstrated.

It has been generally believed that in the Hypotrichida motile organs are confined to the ventral surface (Calkins, 1926; Doflein-Reichenow, 1929; and others). *S. sterkii* then is unique in having cilia on the dorsal surface. On the other hand, careful and complete descriptions have not been made for many species on record, and therefore the presence of cilia may have been overlooked in some cases.

The peristome is a narrow longitudinal groove on the left ventral surface, slightly wider anteriorly than posteriorly. It originates between the left frontal row of cirri and the left end of the transverse row, and extends posteriorly for about two-fifths the length of the body. On the left the peristome is bordered by the membranelles, as already described. An undulating membrane is attached along the right border. The anterior end is often found directly opposite the third cirrus of the right frontal row, that is, when at least three are present in that row. Here the membrane is almost as wide as the peristome, but as it extends backward it gradually tapers to a point. Its posterior extremity extends into the cytopharynx.

The peristome opens into a funnel-shaped cytopharynx (Plate I, Fig. 1). One side of the " cone " is somewhat elongated anteriorly and ventrally it is flattened, forming the thin and transparent floor of the cytopharynx. The posterior portion (or stem of the funnel) extends diagonally across the body within the endoplasm, opening into the interior of the body above the right median row of cirri. The lumen of this posterior cytopharynx is ciliated, and in some specimens stained with hæmatoxylin, the wall appears to be lines with dense strands which retain the dye. Judging from the large size of starch grains often ingested by the organism, the cytopharynx is capable of considerable distension.

The entrance point of food probably accounts for the fact that some organisms were found which are thickest to the right of the main axis. A rapid intake of food, such as takes place after excystment or a period of semi-starvation, would cause the food vacuoles to accumulate there temporarily.

When the body is quite free from food particles, the cytoplasm is pale yellow in colour. The ectoplasm and endoplasm are not visibly differentiated from each other in the living organism. In stained specimens the thin pellicle is apparent, beneath which is a very narrow zone of clear ectoplasm. The remainder of the cytoplasm, or endoplasm, is finely alveolar, and within it lie the food vacuoles.

A conspicuous band of deeply staining granules, irregular in arrangement, sometimes occurs across the entire anterior extremity of the animal (Plate II, Fig. 5). They were seen also within the living organism as coarse refractile granules. The spherules described in connection with the membranelles are quite easily distinguished from them by their definite position and more intense staining property. The significance of the accumulation of these granules in some organisms has not been determined.

In the majority of individuals, four rounded macronuclei lie within the endoplasm. Two are anterior in position and two, posterior (Plate II, Fig. 6). Each has its accompanying micronucleus, which may lie within a distinct depression or near a flattened area of the macronucleus, or free in the endoplasm. The micronucleus is spherical in shape and during its interphase about 2·5 microns in diameter (fixed and stained organism). It is of the massive type.

It must be pointed out here that the free-swimming organisms present a varying picture with respect to nuclei. The process of fission is being studied and will be presented in a later paper. At the present time these studies indicate that each of the two new daughter individuals leaving the cyst wall usually contains four macronuclei and a varying number (2–6) of micronuclei, although frequently four of each type are present. This hypotrich, as stated earlier, divides only during an encysted state and more than one division does not occur. Conjugating individuals have never been encountered.

S. sterkii has one contractile vacuole, located in the endoplasm near the dorsal surface, behind and above the posterior end of the peristome. When the organism is under pressure, a more anterior contractile vacuole may appear in addition to the usual one. An illustration of the elasticity of the pellicle can be seen in connection with the pulsation of this organelle. When the animal is viewed in profile, the expanded vacuole raises the surface like a blister. With contraction the bulge disappears.

The anus is situated at the posterior end of the mid-line. On several occasions, preceding its opening, a vacuole appeared into which an excretory particle was received and then emitted to the exterior.

Habitat and Behaviour.

S. sterkii was collected from a puddle in Chelson Meadow, which, according to Sexton (1924, p. 342), is "a salt marsh near Plymouth reclaimed from the tidal part of the Plym a little more than a century ago, and protected from the tide by an embankment, the accumulation of drainage water being emptied through sluice-gates into the river only at rare intervals." Culture experiments show that the organism thrives equally well in tap water or in brackish water up to a concentration of one part sea-water to one part distilled water. This, of course, is not unusual considering the original habitat just described.

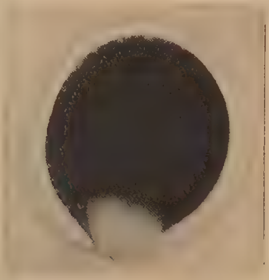
The organism is also otherwise well adapted to life in puddles of short duration. The newly excysted individuals may be exceedingly small, thin, and transparent, but the rate of feeding is so rapid that within a few hours, depending of course upon the amount of food present, their bodies become exceedingly plump. If the first reproductive cyst of an individual of this type is isolated, another division occurs within twelve hours, although the average fission rate seems to be one about every 24 hours. In other words, the organism is able to take advantage of a short favourable period. Further, binary fission takes place at all times within a cyst membrane, and, in many cases at least, the daughter organisms withstand drying.

Protective cysts can be induced at any time by evaporation of the medium, but they may form also when sufficient water is present. The causes of encystment have not been investigated, but even casual observation in connection with the culture of this ciliate convinces one that it is quite sensitive to its environment, and that this sensitivity is often expressed in terms of encystment or excystment.

S. sterkii tends to encyst in groups, as was found to be the case in

Euplotes taylori (Garnjobst, 1928), so that the surface of the watchglass may be sprinkled with grape-like clusters. If complete evaporation of the medium takes place very quickly, or if the medium is removed at once following the formation of a cyst wall, the organism invariably dies. Whether accidental or not, the formation of clusters of cysts would then be of survival value, for cysts more central in position are protected from rapid dessication. This point has not been tested experimentally.

Cyst formation may be observed under the microscope in hanging drop preparations. Both protective and reproductive cysts may be formed if the organisms are chosen at random from a thriving culture. In either case the animal rotates in place until a rounded form is assumed and a cyst wall has been secreted, after which rotation continues for some time within the wall. The reproductive cyst can be recognized while rotation is still in progress, for in these the macronuclei aggregate to form one large central mass, whereas in protective cysts they remain separated from each other. The macronuclear mass soon elongates and this indicates the position of the division plane, which is always at right angles to the elongation. Cytoplasmic division is preceded by the thinning of the macronucleus at its mid-region and final separation into two parts.



Text-fig. 1.—Cyst of *S. sterkii*. Photo-micrograph. Heidenhain's hæmatoxylin stain with very little destaining to show large vacuole. × 638.

Sooner or later ciliary motion within both types of cysts discontinues. Now if the coverslip is placed within a moist chamber for several hours, or overnight, a large fluid vacuole appears, such as is shown in Text-Figure 1. The space between the wall and the dedifferentiated organism is typical also of the living cyst.

Excystment may be induced by the addition of tap or distilled water, either before or after evaporation of the medium, at room temperature. Reproductive cysts which are formed without an accompanying evaporation of the surrounding medium, excyst spontaneously, that is, after the quiescent period ciliary motion again occurs, rotation commences, and in due time two new daughter individuals emerge through the cyst wall.

A detailed description of encystment and excystment will appear in a later paper.

SYSTEMATIC POSITION.

In 1878 Sterki outlined a revision of the Oxytrichina instituting seven new genera, among which was Stylonethes which he characterized as follows :—

" Körper vorn verschmälert, hinten gerundet, stark gewölbt. Auf den vordern Hälfte des Stirnfeldes viele (15–20) zerstreute Wimpern, 2 Bauchwimperreihen, keine Afterwimpern. Die linke Randreihe beginnt auf dem Stirnfeld und überspringt das Peristom."

A single species, named *S. tardus*, was placed within the genus, but no description was given, the reason being that the author intended to give complete details in a later paper. This, so far as the writer has been able to learn, has never appeared.

Kent (1881, p. 782) stated that " so far as is at present possible to determine, this single type (Stylonethes) connects the two genera Holosticha and Uroleptus." Bütschli (1889), on the other hand, temporarily assigned *S. tardus* to the genus Uroleptus. In 1888, Gourret and Roeser described a new ciliate which they named *Stylonethes fusiformis*. The validity of this placement will be discussed below. Recently, Kahl (1932) described a new genus, Paraholosticha, including two species which bear a close resemblance to *S. sterkii*.

There are five distinct characters given by Sterki in his brief description of Stylonethes which are found also in the species herein described and in Kahl's *P. herbicola* and *P. muscicola*, namely, (1) four ventral, longitudinal, uninterrupted rows of cirri ; (2) an anterior transverse row of cirri ; (3) differentiated frontal cirri ; (4) no anal cirri ; and (5) a rounded posterior extremity.

Sterki considered the transverse row as an anterior extension of the left marginal row of cirri which is interrupted by the peristome. Since it is not interrupted by a more or less undifferentiated space, as is the case in some species of the genus Oxytricha, but by the highly differentiated region, the peristome, it seems to the writer more convenient and correct to consider this row a separate one. It is true that Sterki did not designate precisely the location of this row, except to state that it begins on the frontal field. However, it is clear that in *S. tardus* there is present an anterior row of considerable length, otherwise Sterki would not have been able to differentiate these cirri from the scattered frontal cirri, which are quite numerous (15–20). Kahl (1932) in his description of *S. tardus* does not include the statement of Sterki, " Die linke Randreihe beginnt auf dem Stirnfeld und überspringt das Peristom."

Whether the anterior transverse row is of generic significance or not, the remaining four characters are sufficient to distinguish the species under consideration from other genera having few, uninterrupted, longitudinal rows of cirri on the ventral surface. These genera are (1) Uroleptopsis Kahl 1932; (2) Holosticha Wrzesniowski 1878, emend. Entz 1884; (3) Amphisia Sterki 1878, emend. Entz 1884; and (4) Uroleptus Ehrenberg 1831, emend. Stein 1859. The following summary illustrates this point:—

	Frontals.	Anals.	Post. Extremity.
Uroleptopsis	None	None	Rounded.
Holosticha	None	Present	Rounded.
Stylonethes	Present	None	Rounded.
Uroleptus	Present	Pres. in some	Tail
Amphisia	Present	Present	Rounded.

Gourret and Roeser (1888) maintain that the characters of their *S. fusiformis* correspond in all respects to those laid down for the genus Stylonethes by Sterki, except that the marginal cirri are entirely lacking. This difference they did not consider sufficient to place the species elsewhere. If this were the only difference their stand might be justifiable, since in the closely related genera Holosticha and Amphisia, as emended by Entz (1884), there is a slight variation in number of ventral rows. However, it is difficult to understand the row of cirri along the right border of the peristome. These must have been considered the frontal cirri by the authors, otherwise the absence of frontals would certainly have been considered a second, if not an important generic difference. But, because of the similarity in position, it is also possible that they mistook an undulating membrane for a row of cirri; or, they are cilia and not cirri. The description of the ciliation of the peristome is as follows: " Des deux côtés de la gouttière, le droit est un peu plus saillant; il porte des cirrhes plus vigoreux que ceux implantés à gauche " (p. 191). No further mention was made of this anterior row of cirri. Figure 13, Plate XIV is not adequate with respect to the ciliation of the peristome and is not convincing with respect to the presence of frontal cirri. For these reasons it seems to the writer that Gourret and Roeser's *S. fusiformis* cannot be placed with certainty within any genus. Kahl (1932) expressed doubt that it is a hypotrich.

S. sterkii and *P. herbicola* Kahl show a striking resemblance and it is not at all unlikely that they are one and the same species. If so, then *S. sterkii* should be called *S. herbicola* (Kahl). On the other hand, there are differences, according to determinations made from the figure and short description of *P. herbicola* (Kahl, 1932, Fig. 88). These are summarized below :—

S. sterkii.	*P. herbicola.*
1. Length, 94–160μ.	1. 150–190μ.
2. All 4 longitudinal rows of cirri, *except* left median row, extending to posterior extremity.	2. All 4 longitudinal rows of cirri extending to posterior extremity.
3. Anterior transverse row with 12–22 cirri.	3. Anterior transverse row with 15–20 cirri.
4. 3–10 frontal cirri, in 2 short rows.	4. 16 frontal cirri, in 2 short rows.
5. Cirri of ventral surface similar in size.	5. Cirri of anterior transverse row and marginals larger.
6. Dorsal cilia, in 3 longitudinal rows.	6. Dorsal bristles or cilia (?) present.
7. Isolated cirri near right peristomal border.	7. No isolated cirri.
8. Intermembranelles present.	8. ?
9. Dorsal contractile vacuole, above posterior end of peristome.	9. Contractile vacuole some distance posterior to peristome.
10. Macronuclei, 4 ; micronuclei, 4.	10. Macronuclei, 2 ; 1 micronucleus.

Some of these differences may be due to oversight on the part of Kahl. Yet this can hardly be said of his observations regarding the larger size of the cirri of the anterior transverse row, " Ganz nahe dem Vorderrand des Frontalfeldes ein Kranz zahlreicher verstärkter Cirren " (p. 545). Figure 88 shows larger cirri in the marginal rows, although no mention is made of it in the text. In Kahl's general description of the Hypotricha (1932, p. 533), the following statement is made of the marginal cirri, " . . . sie sind öfter etwas stärker als die eigentlichen Ventralcirren. . . ."

It seems impossible to the writer that anyone studying *S. sterkii* even for a short period would not have discovered its cysts. Kahl (1932) does not mention cysts. It is of course understood that a key is necessarily limited in matters of detail. However, in the separation of species if it should be found that in addition to minor differences, one species divides only within a cyst wall and the other does not, the character becomes significant as a specific difference.

The writer has already pointed out that in *S. sterkii* the free-swimming forms present a varying picture with respect to nuclei. According to Kahl, *P. herbicola* has two macronuclei with one micronucleus between. This condition is also found in some free-swimming forms of *S. sterkii*.

Kahl maintains that the most important difference between *P. herbicola* and *P. muscicola* is the presence in the former of two macronuclei and one micronucleus, and in the latter, of two to three micronuclei for each macronucleus. Figure 89 shows two macronuclei with reorganization bands, thus it does not represent the nuclear condition at the interphase. There are, however, other differences, (1) in length of organism ; (2) in the arrangement of the ventral, longitudinal rows ; (3) in length of peristomal field; and (4) the presence of three cirri at the mid-line posterior in position to the frontal transverse row in *S. muscicola*.

It is of no consequence to the writer whether the form herein described is named *S. sterkii* or *S. herbicola*. A detailed description of *S. herbicola* would decide the matter. The key by Kahl (1932) has been available to the writer only very recently through the courtesy of Professor Kirby. Many changes have been made in the genera characterized by few uninterrupted rows of cirri on the ventral surface. The value of these changes can only be determined by those who have a thorough knowledge of the various types involved.

DIAGNOSES.

Credit is due Sterki for having recognized the distinctive characters of the genus which he created, but he also included those which are specific for *S. tardus*. Therefore, it seems desirable to restate the generic characters of Stylonethes briefly as follows:—

Genus STYLONETHES Sterki, 1878

Paraholosticha Kahl, 1932.

Diagnosis: A hypotrich without neck or tail. Ventral surface with four uninterrupted longitudinal rows of cirri. Differentiated frontal cirri present, disposed in rows or scattered. No anal cirri.

STYLONETHES STERKII sp. nov.

Diagnosis: Body highly flexible, elongate-elliptical, anterior end with shallow excavation on left side, widest through middle, width about $\frac{2}{5}$ to $\frac{1}{2}$ of length. Anterior extremity having ventrally, transparent projecting lip; dorsally, membranelles extending sinistrally from termination of right median ventral row of cirri following peristomal border. Dorsal surface elevated, thickest centrally, periphery rounded; with 3 longitudinal rows of cilia. Ventral surface slightly concave with 4 (2 median and 2 lateral) uninterrupted rows of closely-set cirri, median ventrals traversing frontal field. Twelve to 22 cirri form a ventral transverse row immediately posterior to membranelle series. Differentiated frontal cirri in 2 rows between the left median ventral row of cirri and peristomal field; number of cirri in these rows variable—left, 1–5, right, 2–6. One to 3 isolated cirri posterior to frontal cirri and near right peristomal border. Peristomal field narrow, length about two-fifths of body; undulating membrane on right border. Cytopharynx directed obliquely, opening centrally above right row of median ventral row of cirri; ciliated. A dorsal contractile vacuole above posterior extremity of peristomal field. Anal opening at mid-line of posterior extremity. Four macronuclei, two anterior and two posterior. Micronuclei 4, position variable. Binary fission in encysted state only. Length 94–160μ ; width 38–70μ. Habitat, fresh water or brackish. Locality, Chelson Meadow, Plymouth, England.

STYLONETHES TARDUS Sterki 1878.

Diagnosis : Differentiated frontal cirri scattered, 15–20 in number. Two median ventral rows of cirri probably not traversing frontal field. Species without figures and dimensions.

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Nitrates in Aquarium Water.

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It is known that considerable amounts of nitrates accumulate in sea-water which has been circulating in an aquarium stocked with fish and marine animals. An amount equivalent to 1 gram $NaNO_3$ per litre was found in the Aquarium of the Koninklyk Zoölogisch Genootschap Natura Artis Magistra in Amsterdam.

These amounts of nitrate are never found in natural sea-water and whereas it is not quite certain whether such quantities of nitrates themselves are absolutely harmless, they cause a decrease in pH by substituting CO''_3 and HCO''_3 ion by NO'_3, and they may lead to an undesirable formation of injurious nitrates as is described below.

The rate of production of nitrate and dissolved phosphate was followed in a tank stocked with fish, having a capacity of 1·3 cubic metres. During a month when the water was being continuously passed through a filter at a rate of 20 cubic metres per hour, the production was found to be 12·4 mg. nitrate-nitrogen per litre and 0·87 mg. P_2O_5 per litre. During the following month when the filter was kept out of action and the air supply carefully regulated, the production was found to be 10·6 mg. nitrate-nitrogen and 0·24 mg. P_2O_5 per litre. At the end of the month the water became turbid and had to be filtered.

Provided the water is aerated, the ammonia (which never amounts to more than 0·1 mg. per litre daily) originating from the breakdown of albuminoids is oxidised by nitrifying bacteria to nitrites and nitrates, a process which is stimulated by a small amount of organic matter and is not affected by filtration.

The reverse process—the reduction of nitrate *via* nitrite to nitrogen—is not likely to occur in water nearly saturated with oxygen and containing only a small amount of dissolved organic substances, although denitrifying bacteria are always present.

An experiment was made in which the organic substances suitable as food for the last-mentioned bacteria were increased. A tank stocked with fish, having a capacity of 1·3 cubic metres of sea-water was brought to a pH of 8·2 by the addition of lime, and a quantity equivalent to the addition of 0·6% of sodium lactate dissolved in it. The water in the tank was then kept continuously passed through a filter and was thoroughly aerated. Analyses were made at frequent intervals of the ammonium, nitrite, nitrate, total nitrogen and phosphate content of the water. A measure of oxidisable organic matter present was obtained by titrating with decinormal potassium permanganate. The estimations were made in the water that flows directly from the filter (F) and in the water in the tank (B). F is therefore the purified water, B the water contaminated by the fishes.

After the addition of lactate the water became turbid and a considerable amount of nitrite was found in the water, while the amount of nitrate and of total inorganic nitrogen decreased, as shown in the Table. It is considered that the added lactate caused the denitrifying bacteria to develop. Later, when the lactate had been partly used up, the analyses showed oxidation of nitrite to nitrate to be taking place. The increase in nitrate started some four days after the addition of lactate, when the value for oxidisable organic matter had fallen to about 30. It is considered that an equilibrium is attained at a given moment between the activities of the denitrifying and the nitrifying bacteria and that nitrite appears when the denitrifying bacteria have insufficient lactate left. After a second addition of lactate on the 16th, the remaining nitrite and nitrate rapidly disappeared.

Throughout the experiment the concentration of ammoniacal nitrogen remained low, the ammonia formed being rapidly and almost completely oxidised. Repetition of the experiment after addition of potassium nitrate to the water gave a similar result. It was also found that, instead of lactate, tartrate may be used and that without filtration the water remained turbid and that denitrification was neither so quick nor so complete.

The turbidity is caused by bacteria, both cocci and rods. After the treatment with lactate followed by the disappearance of nitrates, the water supported fish life in a healthy condition.

SUMMARY.

The formation of nitrate in the water of an aquarium tank stocked with fish was followed. As much as 1 gram per litre expressed as sodium nitrate was found.

By adding lactate or tartrate to the water the development of denitrifying bacteria brought about almost complete removal of the nitrates and nitrites in the water.

The experiments form part of an investigation made under the direction of Dr. Jan Smit.

TABLE I.

SEA-WATER FILTERED UNDER ADDITION OF LACTATE.

Date.	Temp. °C	·pH	Water.	NH_3N mg./L.	NO_2N mg./L.	NO'_3N mg./L.	Total Inorg.N mg./L.	Org.N. mg./L.	P_3O_5 mg./L.	$KMnO_4$ c.c.O.In/L.
28.5.32	15·5°	8·2	clear	0·2	0	53·5	58·7			
		8·2	,,	0·3	trace	59·2	59·5			
1.6.32	16°	8·2	,,	0·20	,,	58·5	58·7	0·26	3·96	4·84
		8·2	,,	0·16	,,	58·5	58·7	0·53	3·96	4.84
4.6.32	16·5°	8·2	,,	0·16	,,	37·1	37·3		3·65	40
		8·2	,,	0·27	0	53·8	54·1		3·65	40
6.6.32	16°	8·1	turbid	0·28	4·87	24·7	29·9			58
		8·1	,,	0·23	2·74	26·9	29·8			80
7.6.32	16°	8·1	,,	0·33	12·4	1·3	14·0			30·2
		8·1	,,	0·51	11·3	2·4	14·2			34·0
8.6.32	16°	8·1	,,	0·77	12·2	2·2	15·2		1·90	28·6
		8·1	,,	0·50	12·2	2·8	15·5		1·90	30·2
11.6.32	16·5°	8·1	,,	1·59	12·5	6·9	21·0		2·00	26·5
		8·1	,,	1·27	12·1	6·6	20·0		2·00	27·5
13.6.32	18·5°	8·1	clear	0·80	14·6	7·3	22·7		2·56	26·9
		8·1	,,	1·06	14·6	7·3	23·0		2·56	27·1
15.6.32	18·5°	8·2	,,	0·26	12·3	11·9	24·5	4·44	2·83	24·6
		8·2	,,	0·22	12·3	10·5	23·0	2·72	2·83	25·1
16.6.32	19°	8·2	turbid	0·24	9·6	0	9·8		2·07	96
		8·2	,,	0·20	11·4	2·7	14·3		2·17	117
18.6.32	19°	8·2	,,	0·26	0	0·12	0·38		2·17	109
		8·2	,,	0·25	0	0·12	0·37		2·17	108
20.6.32	17°	8·2	,,	0·17	0	0	0·17	1·22	2·13	55·8
		8·2	,,	0·16	0	trace	0·16		2·13	56·2
22.6.32	16·5°	8·1	clear	0·28	0	0·18	0·46		2·47	58·1
		8·1	,,	0·39	0	0·07	0·46		2·40	60·3
30.6.32	18°	8·1	,,	0·51	0	0·6	0·57		1·82	10·8
		8·1	,,	0·58	0	0·6	0·64		1·88	11·0

→ Addition of organic substance.
F = filtered water.
B = water in the tank.
(The difference between the values of F and B on the same day is affected by the filtration.)

The Use of a Selenium Rectifier Photo-electric Cell for Submarine Photometry.

By

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and

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With 1 Figure in the Text.

Photo-electric cells of the rectifier or "Blocking-layer" type possess such manifest attractions from the point of view of convenience that they have come into wide use for the measurement of illumination, especially for artificial light and for use as exposure meters. Several photometers making use either of the cuprous oxide cell of Lange (1930), or of the selenium cell of Bergmann (1931), or of that of Bernheim, the composition of which is as yet undisclosed, are now on the market for such purposes. Many, if not all, of these are graduated on the assumption that the current is related to the illumination by a rectilinear proportion; such a proportionality holds approximately for the relatively feeble illuminations met with indoors, when the galvanometers used are of low resistance. The cells have, however, in several instances been used for measuring daylight in the open without paying attention to the fact that, under such conditions, the illumination–current relationship is not rectilinear. We have already (1933, 1) gone into these and other precautions required in the use of rectifier cells, and have found (1933, 4) that for a Bergmann cell made by the Weston Electrical Instrument Co. the curvature of the illumination–current characteristic could be allowed for with sufficient accuracy by dividing the current in micro-amperes, C, flowing through a 10-ohm galvanometer, by $1-0{\cdot}003\times\sqrt{C}$, the use of a divisor in place of a multiplying factor being more convenient, in this instance, for slide rule working; alternatively, a curve may be constructed from the formula to reproduce that found by experiment. Owing to its great sensitivity the cell, under opal-flashed glass, may give a current of over one milliampere at noon in the open late in January, when set horizontally. This must be divided by 0·905 to correct for curvature of characteristic, so that a current of 1·00 milliampere corresponds to a true illumination of 16·0 thousand metre candles ; this would appear to be 14·4 if uncorrected. The figures are given on the " selenium, arc, scale," namely using a carbon arc to standardize the selenium cell. With summer illuminations of 50–100 thousand metre candles the difference between the true and the uncorrected illumination would be more serious.

It follows from this that, if such a rectifier cell be used for the permanent recording of daylight, corrections would need to be applied to the record charts. This effect might be greatly reduced (probably to negligible size) by mounting the cell so that it only received a small fraction of the light transmitted by a diffusing window and by then using a sensitive instrument to record the small currents obtained with this relatively feeble illumination.

The effect is generally negligible with vacuum emission cells, provided sufficient anode potential be applied to ensure saturation in the brightest light.

For measuring under-water illumination, rectifier cells were used by several workers almost simultaneously. We used a cuprous oxide cell (1933, 3) in the summer of 1932, making use of a 10-ohm galvanometer for measuring the current. The galvanometer was on land, the cell being carried by a diver. For use at sea it was proposed to use the potentiometer-telephone method to measure the open circuit voltage, the illumination–voltage relationship for which was found to show a very pronounced curvature. The cuprous oxide cell has since been abandoned as much inferior to the selenium rectifier.

Pearsall and Ullyott (1933) used a Bernheim cell in Lake Windermere, and give a comparison between its readings and those of a thin-film potassium on copper vacuum cell for February 8th. The Bernheim cell has a high sensitivity and a greater blue sensitivity than the selenium cell. A pointer galvanometer was found suitable for work from a small boat on the lake.

The most extensive series of measurements in the open sea with a rectifier cell were those carried out by Utterback and Boyle (1933) upon waters in and outside Puget Sound and up the coast towards Alaska ; they worked in a small steamer, and used the Leeds and Northrup marine galvanometer ; this is a mirror galvanometer with a specially robust suspension. To provide sufficient sensitivity a very powerful field is used, produced by an electro-magnet. The latter operates from a 6-volt circuit and takes half an ampere. Utterback found this quite satisfactory with the Bergmann-Weston cell, and worked down to 50 m., using colour filters for the various regions of the spectrum and an ingenious electrically operated filter-changing mechanism.

In the Baltic Pettersson and Landberg (1934) used a selenium cell of the Bergmann type, constructed or modified by Lange, which, they state, has a maximum of sensitivity rather in the green than in the yellow orange as usual. This they used with a pointer galvanometer which worked well in their calm water. They found it necessary to use a screen to limit the illumination of their cell in strong light.

Our own work was carried out with two Bergmann-Weston selenium cells, one mounted on the deck-house roof, and the other in the small gun-metal case previously used for the cuprous oxide cell. With this we have made some preliminary measurements of the penetration of light of various colours into sea-water 1–2 miles south-east of Plymouth Breakwater.

The Standardisation and Use of Rectifier Cells.

We have dealt elsewhere with the optical conditions affecting a submerged photometer (1933, 2), and with the testing and behaviour of rectifier cells in bright light (1933, 1). It is only necessary to state here that the reading of a submerged photometer must be multiplied by 1·09 to correct for the nett effect of variations in internal and external reflections at the surface of the opal window, and that we must allow for the curvature of the current—illumination characteristic of the cell, which curvature becomes more pronounced as the resistance in series with the cell is increased. As high resistance also increases the error due to temperature variation of the cell, it is desirable to use a measuring instrument with the lowest possible resistance. The temperature variation error has been fully studied by Lange (1931).

For work on shore in comparatively bright light we have found a Cambridge Unipivot "Versatile" pointer galvanometer very suitable, as its resistance is only 10 ohms and 1 scale division (readable to 0·1) corresponds to 2 micro amperes, i.e. to about 30 metre candles with the opal glass in position. For strong light a special shunt designed to maintain the effective resistance at 10 ohms (1933, 1, p. 538) may be used.

For weak light, however (say below 500 m.c. or 0·5% of full noon sunlight), a more sensitive instrument is advantageous, and this will probably entail a higher resistance. This is not a serious drawback as the curvature of the characteristic is comparatively small in weak light, and can be corrected for if the requisite data for the given galvanometer resistance has been obtained by photometer bench tests (1933, 1) or by comparison with a vacuum emission cell (1933, 3).

We have not so far attempted to use a galvanometer at sea, as the comparatively small currents obtainable in deep or turbid water, especially with colour screens in use, would require a rather costly and sensitive instrument. We found it more convenient to employ our potentiometer-telephone method (1928, 1933, 2) which was available, rather than to attempt to fit up a system of gimbals sufficiently perfect to enable such a galvanometer to be used on board the trawler *Salpa*. We were not at the time aware of the existence of the special marine galvanometer. The only modification required in the apparatus was the reduction of the resistance through which the current from the cell passed, and across which the potential difference was measured by means of the potentiometer. In the measurements described below this resistance was made 10, 100 or 200 ohms according to the brightness of the light to be measured, but subsequent experience has shown that values of 1000 or 10,000 ohms may be used in weak light, provided that suitable calibrations are effected. This means that for bright light with 10-ohm resistance one potentiometer scale division (10^{-4} volt) corresponds to about 150 m.c., while in weak light the sensitivity can be instantly increased as much as 400 times. There is evidently a limit to the gain of sensitivity obtainable in this way, as, even in very weak light, a large resistance reduces the current passing through ; in fact the maximum P.D. available is the open circuit P.D. of the cell under the given illumination. This might be used, if desired, to measure very weak light, but this method would not increase the sensitivity greatly above that obtainable with 10,000 ohms in circuit.

A curve for the open circuit P.D. of a cuprous oxide cell has already been given (1933, 3).

It is, however, doubtful whether the rectifier cells available at present can be used at considerable depths in the ocean, such as 180 m. (Clarke, 1933), at which emission cells have been used. This doubt arises from the fact that though on open circuit the rectifier cell is rather more sensitive than the emission cell over 100,000 ohms, yet the latter may be used over 1 or 2 megohms. Furthermore, the potassium cell is most sensitive just where the water is most transparent, whereas the selenium cell has its maximum in the orange yellow.

For a typical Weston cell, with opal window, photometer bench tests have shown that the following resistances are convenient :

For currents up to $2{\cdot}5\mu$a (c. 110 m.c.) 10,000 ohms, giving about $2{\cdot}5 \times 10^{-4}$ volt per m.c.

For currents up to 50 μa (c. 1050 m.c.) 1,000 ohms, giving about $0{\cdot}5 \times 10^{-4}$ volt per m.c.

For currents up to 500 μa (c. 8500 m.c.) 100 ohms, giving about $0{\cdot}06 \times 10^{-4}$ volt per m.c.

For currents over 500 μa (c. 8500 m.c.) 10 ohms, giving about $0{\cdot}006 \times 10^{-4}$ volt per m.c.

The calibration curve corresponding to the cell and the resistance must be used to find the value of the illumination.

For further work we have had constructed, by Messrs. Tinsley & Co., a plug-in resistance set, so arranged that the potential difference measured can be across 10, 100 or 1000 ohms according as a single plug is inserted. This aids rapidity of work, for while the air illumination is measured across 10 ohms the under-water illumination may be across 1000 ohms. Spare terminals and a spare plug-hole permit the use of 10,000 ohms already in the potentiometer-telephone apparatus as part of the subdivided 100,000 ohm set.

The potentiometer method seems to be very suitable for work with rectifier cells. The absence of high potentials removes all insulation troubles, and the lowness of the resistance across which the P.D. is measured, as compared with the high value (100,000 ohms) generally needed with emission cells, renders the potentiometer balance very sharp. It could generally be set to within 0·2 scale division, viz. 20 microvolts, when the light was steady enough.

The surface illumination was measured by a cell mounted (under opal glass) on gimbals on the deck-house roof. This was the actual cell used in the laboratory and sky light measurements already recorded (1933, 1, 4), so its characteristics for various series resistances were known. The cell used under water has not, as yet, been tested in this way, but for these preliminary measurements, under conditions in which great accuracy was hardly attainable, we may, without serious error, take its curvature corrections for various resistances to be the same as those for the " deck " cell. The two were almost the same in sensitivity.

The deck cell had been standardised against a carbon arc by the method already described (1928, p. 460), and also against a standard vacuum lamp at a colour temperature 2360° K.—the former gave 14·4 m.c., and the latter 15·1 m.c. per μa for the cell under opal glass exposed to weak diffuse light. The agreement shows the general similarity that this cell bears to the eye in its estimate of the relative brightness of sources of different colours. This is the first cell that we have found that can be standardised against a bare filament lamp and used to measure daylight without obtaining a scale of values utterly different from the visual one. This is a very great advantage, as the arc cannot be regarded as either a convenient or an accurate standard, though it possesses the advantage of readily providing high intensities. Some preliminary tests have indicated that winter daylight with low sun (February 15th, 1934, 15.30 G.M.T.), which was recorded as 15,850 m.c. by a vacuum potassium cell standardised against the arc, was measured as 12,400 m.c. by the Weston cell standardised against the standard filament lamp. Daylight measurements on what we may briefly call the " Selenium, 2360°, Scale " as used below, should, therefore, be about 78 per cent of the corresponding values on the " Potassium, Arc, Scale " which we have hitherto employed. The ratio of the two scales will, however, depend on the colour of the light, and hence on the relative proportion of direct sunlight, the selenium cell being relatively more sensitive to sunlight and the potassium cell to blue sky light.

SUBMARINE MEASUREMENTS.

One group of five series of readings was made a couple of miles south of Plymouth Breakwater on October 10th, 1933.

The usual procedure was adopted, sets of alternate readings of the deck and sea cells being made with the latter suspended from a spar projecting about 2·2 m. clear of the ship's counter, first with the cell about 1 m. above the surface, where the shading due to the ship was small, and then at depths of 1, 5, 10 and 15 metres. Consistent readings could not be obtained at less than 1 m., and the available depth did not allow of working below 15 m., in fact on two occasions the photometer touched the bottom and had to be hauled up a metre or two.

Series were obtained with the cells covered only by opal glasses, and also with blue, green, yellow, and red, filters placed beneath the opal glasses of each photometer, so that the transmission of each filter was independent of the average obliquity of the incident light. The following are particulars of the conditions under which this group of series was obtained :—

Group W.1., including series W.1, W.1.B., W.1.G., W.1.Y., and W.1.R., October 10th, 1933. Drifting W. from position ½ mile W. of Mewstone. Light variable, blue sky and white clouds, β* about 2·0 at 12.42 G.M.T. Wind E., moderate to fresh. Easterly swell. High water 6.51 G.M.T., tide flows to the W. until 2 hours after low water.

W.1. No colour filters. 11.21–12.01 G.M.T., commencing near Mewstone. Vertical surface illumination 45 to 71·5 thousands of metre candles (selenium, 2360°, scale). Touched bottom at 15 m.

W.1.B. Chance's No. 7 blue filters, 13.05–13.25 G.M.T. (just after low water), commencing near Mewstone. Secchi disc visible to 9·5 m. at 13.11.

W.1.G. Corning "sextant green" filters, 13.41–13.59 G.M.T., commencing near Mewstone. Touched bottom at 15 m.

W.1.Y. Sea cell, Chance's No. 4 orange filter. Deck cell Corning H.R. yellow, 14.9–14.50 G.M.T. Further W. than W.1.G.

W.1.R. Schott R.G.1 red filters, 15.05–15.21 G.M.T. Wind lighter. Further W. than W.1.Y.

The results are plotted in the figure on a logarithmic scale as percentages of the vertical surface illumination of the same colour. It will be noted that they all indicate a somewhat large surface loss, which is not unusual with strong winds. Surprisingly clear water seems to have been encountered during the 5-m. readings of series W.1.B., otherwise the results are in accordance with what we should expect for inshore waters, where green light is generally found to penetrate best (1933, 2). It is worth noting that the vertical absorption coefficient μ_v for series W.1.B,

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* As before β denotes the ratio of light from sun plus sky to that from sky alone, receiving surface being set horizontally.

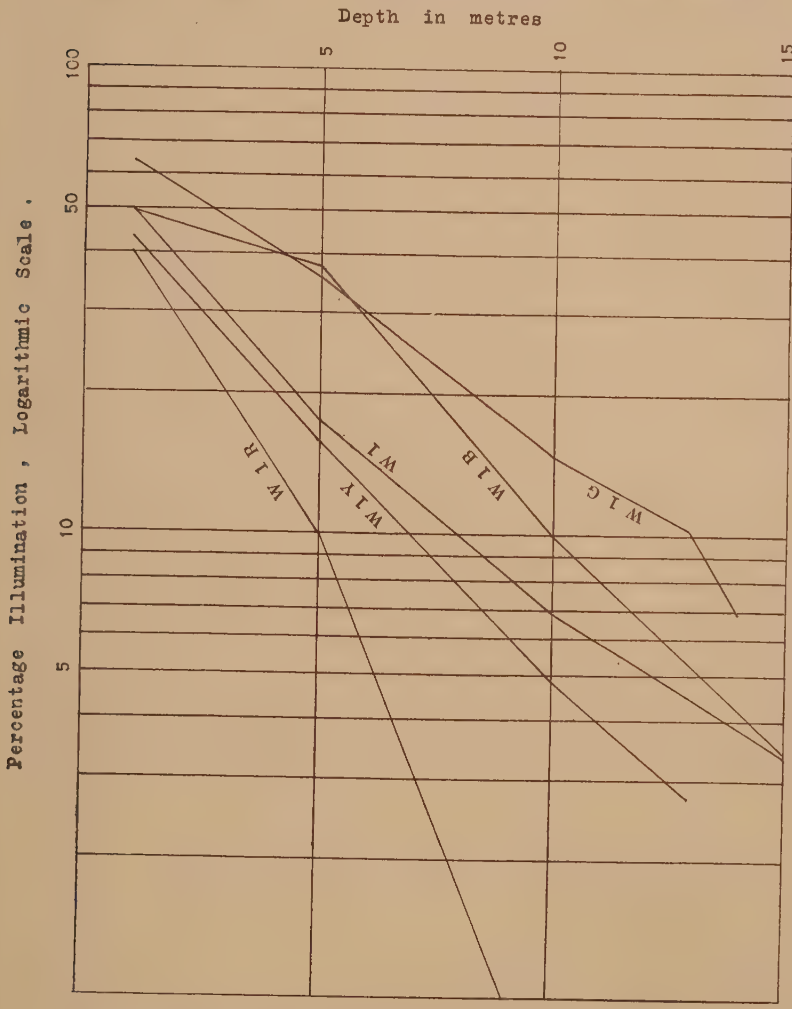

Fig.—Percentage submarine illumination near Mewstone, off Plymouth, October 10th, 1933. The mean vertical absorption coefficients calculated between one and ten metres are: opal only 0·216; blue under opal, 0·177; green under opal, 0·153; yellow under opal (including red), 0·243; red under opal, 0·345.

(1–10 m.) viz. 0·177, agrees almost perfectly with the value 0·179 found by the rough rule $\mu_v = 1\cdot7/D$ which we have previously found applicable as a correlation between μ_v for blue light and D, the maximum depth of visibility of the Secchi disc.

The results shown in the figure agree well with certain of our previous determinations on inshore waters in 1931, carried out at about 1–2 miles off the shore in Whitsand Bay, to the west of Plymouth Sound. These were made using an emission cell, thin-film caesium type CMV6 with colour filters The table shows that the water was slightly clearer for the August 1931 measurements. The filters were the same for the red and green in each year, and very similar in the other cases.

TABLE I.

Showing the Depths in Metres at which the Air Illumination is Reduced, in Water, to 10 per cent. The series numbers refer to the 1931 measurements only, since all the 1933 results are given.

Filter. Series	Blue. 80B	Green. 72G	Yellow. 71Y	Red. 74R	" White." 68H
1931	10·6	14·6	8·0	5·0	7·4
1933	9·9	13·0	7·0	5·0	7·9

Only in the " white " column does the water appear clearer in 1933 than in 1931. This column for 1931 represents the thin-film caesium cell, with a heat-absorbing filter, light green in tint ; this renders its sensitivity nearly uniform over the visible spectrum and absorbs the near infra-red to which this cell is very sensitive. The figures indicate, however, that the selenium cell, which has a maximum sensitivity about 590 mμ, is relatively slightly more sensitive to green light, which penetrates best, than the CMV6 cell with heat-absorbing filter.

The values of percentage illumination given in the table are actual values, read off from the graphs, but as measures of clearness of the water the comparison is not exact, since the surface losses were not the same on the different dates. The general agreement is, however, quite evident.

SUMMARY.

1. Measurements of the penetration of light of various colours into the sea were carried out by means of a selenium rectifier cell. The mean vertical absorption coefficients were : for blue, 0·177 ; green, 0·153 ; " white," viz. no filter, 0·216 ; yellow, 0·243 ; red, 0·345. The results accord well with those obtained under similar conditions with emission cells and show that, for water a couple of miles offshore, green light penetrates best.

2. The current was measured using the potentiometer-telephone method as for emission cells, but determining the drop in potential across

a low resistance, 10, 100, or 1000 ohms. The motion of the ship was too violent to permit of the use of any available galvanometer of adequate sensitivity.

3. Rectifier cells are more convenient to use than emission cells, as the currents to be measured are much larger and the absence of high potentials greatly simplifies all insulation problems. On the other hand the curvature of the illumination–current relation involves additional labour in standardizing and in calculating results.

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Hydrography of the Mouth of the English Channel, 1929–1932.

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With 7 Figures in the Text.

Since 1921 hydrographic data have been collected by the S.S. *Salpa* and several merchant vessels, the records being published in the *Rapport Atlantique* and the *Bulletin Hydrographique* each year. A description of the conditions in the mouth of the Channel –the varying temperature, salinity, and movements of the water masses—during the years 1925 1928 was published in this Journal, Vol. XVI., pp. 791–820, and included a review of the objects of these investigations and the methods used in working up the collected data. This present publication forms a continuation of this. The same methods of dealing with the data have been used.

Temperature Distribution.

Diagrams showing the distribution of temperature with depth at the International Station E1 for the years 1930, 1931, and 1932 are shown below, that for the year 1929 having been included on page 801, Vol. XVI. These three years are not remarkable, except that the water in the autumn of 1931 was warmer than any of the previous years except 1921. This cannot be attributed to an inflow of warmer Atlantic water such as occurred in 1921, because at this time the mouth of the Channel was of unusually low salinity.

Salinity Distribution.

Charts showing the distribution of salinity at the beginning of each month have been prepared from isopleth diagrams of the data as in previous years. A selection of these is reproduced in Figures 3–7, and illustrates changes which have occurred during the four years under review. It has been clear throughout that such charts only give a rough picture owing to the limited intensity of sampling, and, furthermore, that the isohalines are not smooth contours, but that numerous offshoots, lacunæ and isolated patches exist. The data shown in Figure 2 confirm this deduction.

However, in spite of this and the fact that a personal equation comes in when drawing the salinity diagrams, each one gives a consistent generalised picture. A number of such diagrams were drawn for fortnightly intervals, without reference to the diagram for the preceding and subsequent fortnight. Arranged in order these pictures gave a reasonable

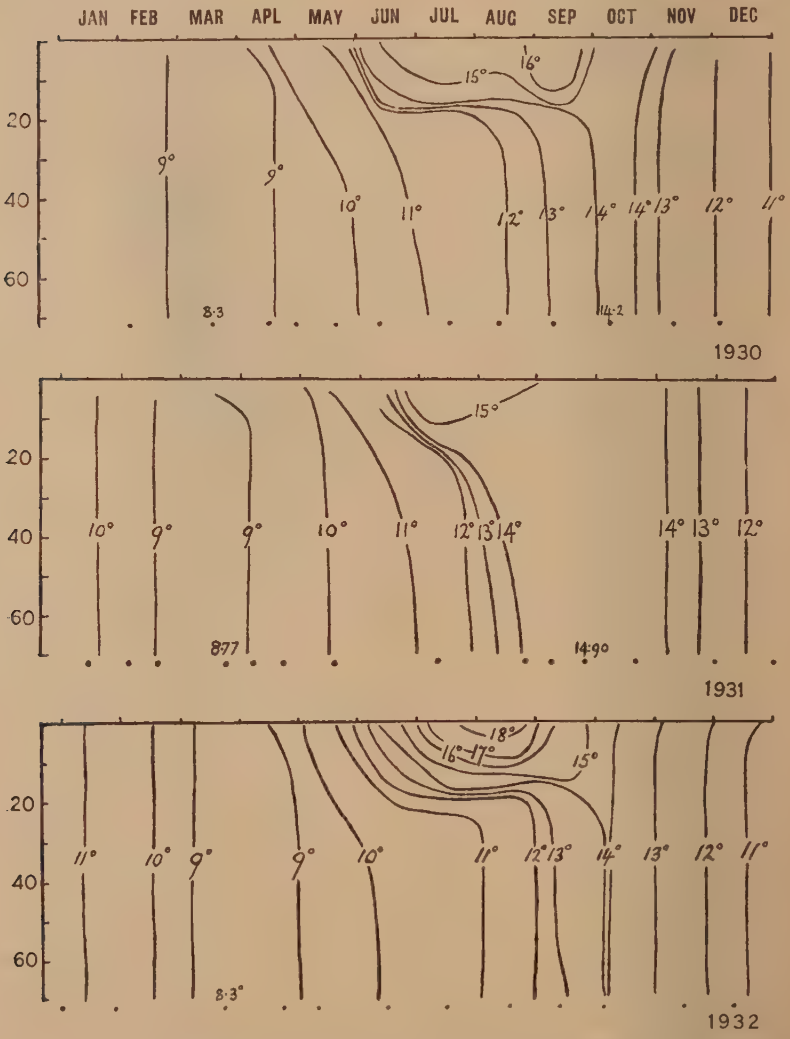


Fig. 1.—Isopleth diagrams showing distribution of temperature with depth (in metres) at Station E, from January, 1930, to December, 1932.

sketch of the general distribution, for if it had been otherwise diagrams for consecutive fortnights would not have been consistent.

The general circulation of the water masses in the area may be outlined. There is usually a slow drift of water through the Channel and out into the North Sea, undergoing gradual dilution as it passes eastward from the Atlantic. This east-going drift is sometimes held up and even reversed by northerly and easterly winds (Carruthers). At times Atlantic water in large quantity enters the mouth of the Channel in the form of a tongue, the water which it displaces moving out north-westward past Lands End. Sometimes the tongue penetrates far up Channel in the east-going drift, either as a ribbon or as patches. More often the high salinity water forming the tongue moves out north-westward past Land's End, its place being taken for the most part by water of lesser salinity from the Atlantic and the west coast of France, and only a small moiety of it passes up Channel. On occasions the mouth of the Channel has filled up with quite low salinity water passing in round Ushant from the west coast of France (April–May, 1928, and again apparently in July, 1931), the water which it displaced having of necessity moved out north-westward for the most part.

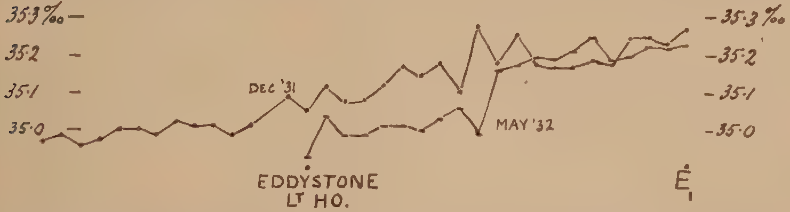


Fig. 2.—Diagram showing salinity of surface samples taken at half-mile intervals on the line Plymouth–Eddystone–International Station E_1, on December 31, 1931, and May 10, 1932.

Throughout the period under review current measurements have been made at the Varne Lightship and the movement of water into or out of the North Sea calculated for each month. I am indebted to Dr. J. N. Carruthers for these data.

The change in salinity distribution indicates during some months a passage of relatively high salinity water up Channel and during others a hold-up or even reversal. It could not be expected that they would every month reflect the nature of movement through the Straits of Dover, although this frequently occurred. The notable exceptions were that in July, 1931, there was a flow through into the North Sea, whereas the salinity distribution suggests a hold-up or reversal ; again it was deduced from the salinity distribution that a flow into the North Sea was resumed during the latter part of October, 1931, whereas this did not happen until the beginning of November.

The changes and deductions may be epitomised as follows, where, for the sake of brevity, water above 35·3°/$_{oo}$ salinity is termed Atlantic water.

1929.

During January and February Atlantic water in the Channel moved out north-westward past the Lizard and also up Channel.

March. Little or no change.

April. Atlantic water moving out north-westward past the Lizard. East-going drift through Dover Straits held up by easterly winds.

May. Atlantic water entering mouth of Channel past Ushant.

June, July, August, September, October, November. Gradual penetration of Atlantic water into mouth of Channel.

December. Notable east-going drift up Channel.

1930.

January. Movement up Channel. A patch of high salinity water 35·3–35·4°/$_{oo}$ occurred north of the Channel Islands during this month.

May. Appearance of high salinity water on the line Land's End–Ushant in the middle of the month and of remarkably high salinity water, 35·5–35·7°/$_{oo}$, at the end of the month.

Water of 35·8°/$_{oo}$ occurred at Seven Stones light vessel at end of month.

A stratum of water with salinity 35·6–35·7°/$_{oo}$ was found by H.M.S. *Beaufort* at 50° 08′ N. 6° 15′ W. at a depth of 50 metres, with water of lesser salinity above and below. A stratum with salinity 35·5–35·59°/$_{oo}$ found by S.S *Muirchu* on May 15 at 50° 55′ N. 9° 56′W. with water of lesser salinity above and below.

June. Gradual penetration of the very high salinity water into mouth of Channel, a patch having salinity 35·75°/$_{oo}$ being encountered early in July on the line Plymouth–Guernsey.

July. Retreat of the very high salinity water, probably north-westward past the Scillies.

August. Penetration of Atlantic water into mouth of Channel ; rather marked movement of water through Dover Straits.

September and October. Continuation of the movements experienced in August but less marked ; passage of Atlantic water out north-westward past Lizard.

1931.

November, December, 1930, January, February. Atlantic water seems to have been replaced largely by low salinity water moving in past Ushant from the French coast. Patches of Atlantic water meanwhile passing up Channel.

March. Water of relatively high salinity, 35·4–35·58°/$_{oo}$, appeared on the line Land's End–Ushant at the beginning of the month and again towards the end of the month.

April, May, June. Patches of high salinity water passing eastward up Channel. Reappearance of high salinity water on the line Land's End–Ushant at beginning of June.

July, August. Mouth of Channel filled with water of unusually low salinity.

September, October. Passage up Channel and through the Straits of Dover held up or reversed by easterly winds.

November. Water from Atlantic entered mouth of Channel. Passage westward through Straits of Dover resumed.

December. Atlantic water entered mouth of Channel.

1932.

January. Water of 35·4°/$_{oo}$ salinity and greater observed off the mouth of the Channel. Marked passage into North Sea through the Straits of Dover.

February. Water of 34·4–35·5°/$_{oo}$ observed off mouth of Channel. A patch having salinity exceeding 35·5 moved up Channel as far as 3° W. Passage of water into North Sea held up or reversed.

March. Atlantic water moves out from mouth of Channel.

April. High salinity water reappears north of Ushant, 35·5%°, and Atlantic water penetrates into Channel. Passage into North Sea took place.

May, June. Patches only of high salinity water observed within the Channel. During June passage into North Sea held up.

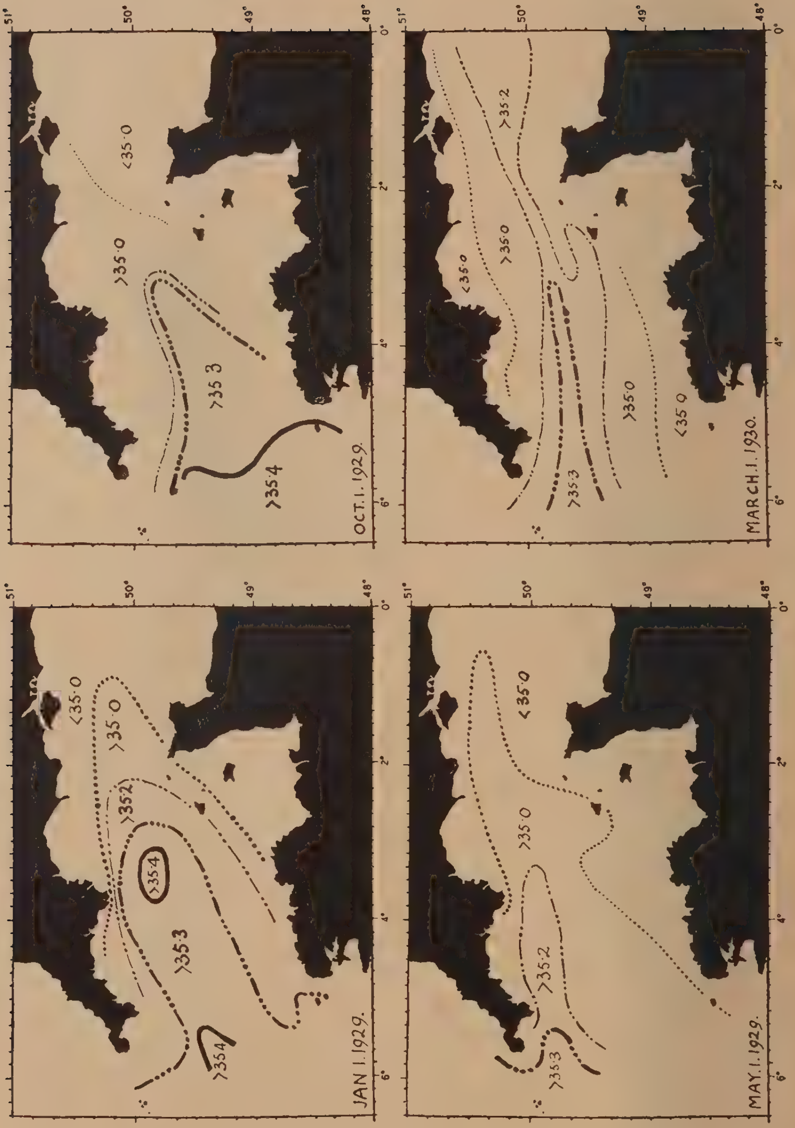
July. Water of lower salinity filling mouth of Channel, high salinity water off the mouth. Water of 35·5–35·6°/$_{oo}$ observed south-west of Ireland. Passage into North Sea took place.

August, September, October. Water of relatively low salinity fills mouth of Channel; high salinity water observed across the mouth. A notable passage of water into the North Sea took place in October.

November. Atlantic water penetrates mouth of Channel and high salinity water observed across the mouth.

December. Water of high salinity, 35·5–35·6°/$_{oo}$, observed at entrance during early part of month. A passage of water into the North Sea took place.

The notable conditions during this period were the relatively low salinities and high temperatures during the latter part of 1931, and the frequent occurrence of unusually high salinity water off the mouth of the Channel at intervals during 1931 and 1932.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JAN. 1. 1929.
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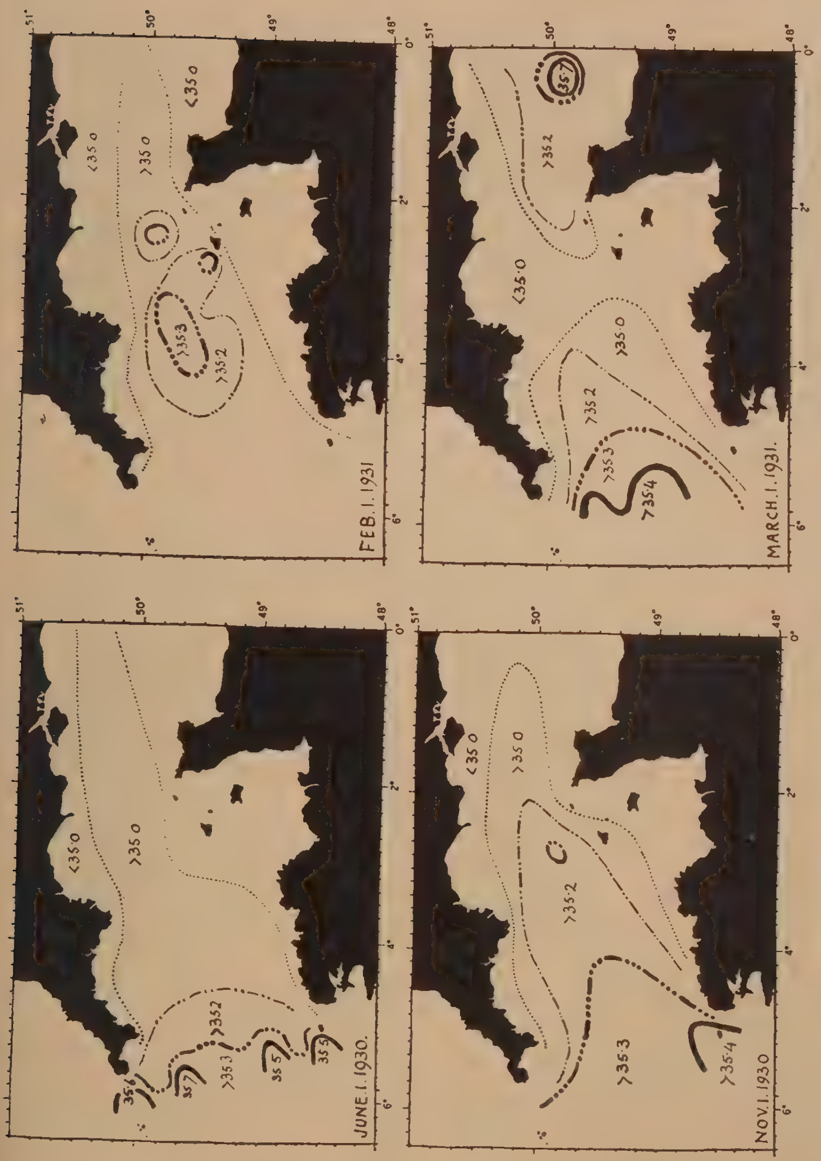
FIG. 3.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MARCH.1.1931.
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JUNE.1.1930.
<35·0
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FIG. 4.

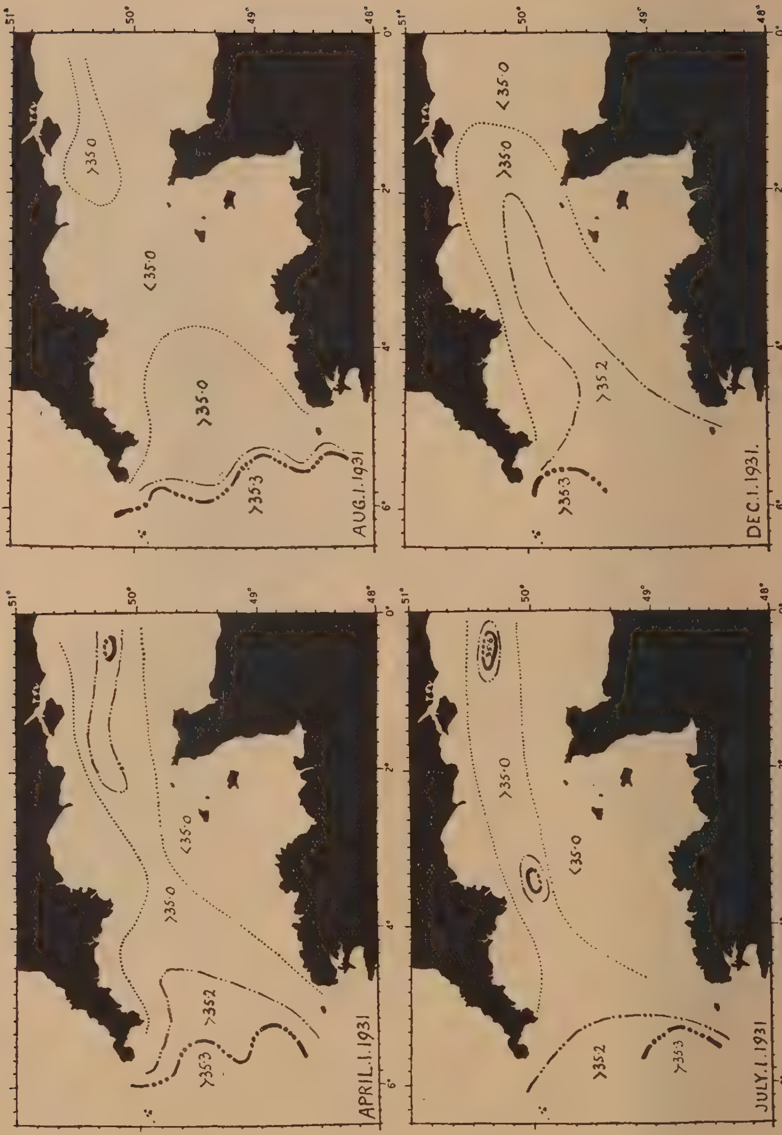
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Fig. 5.

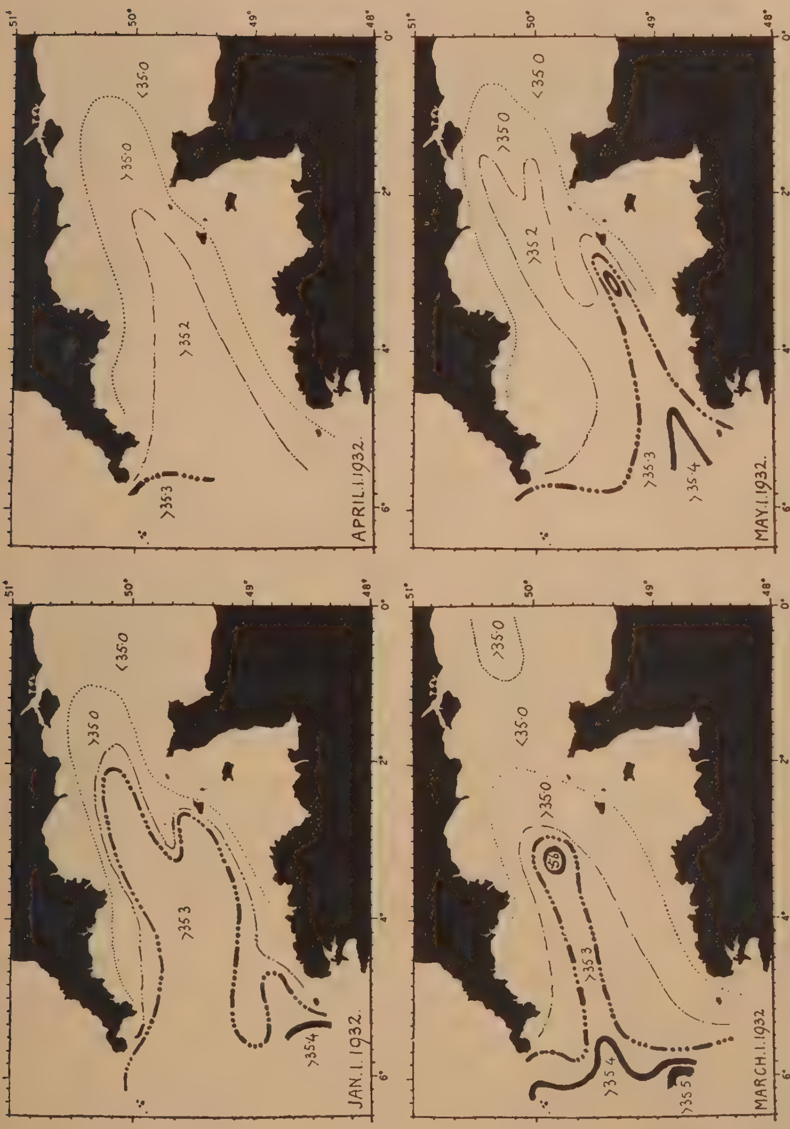
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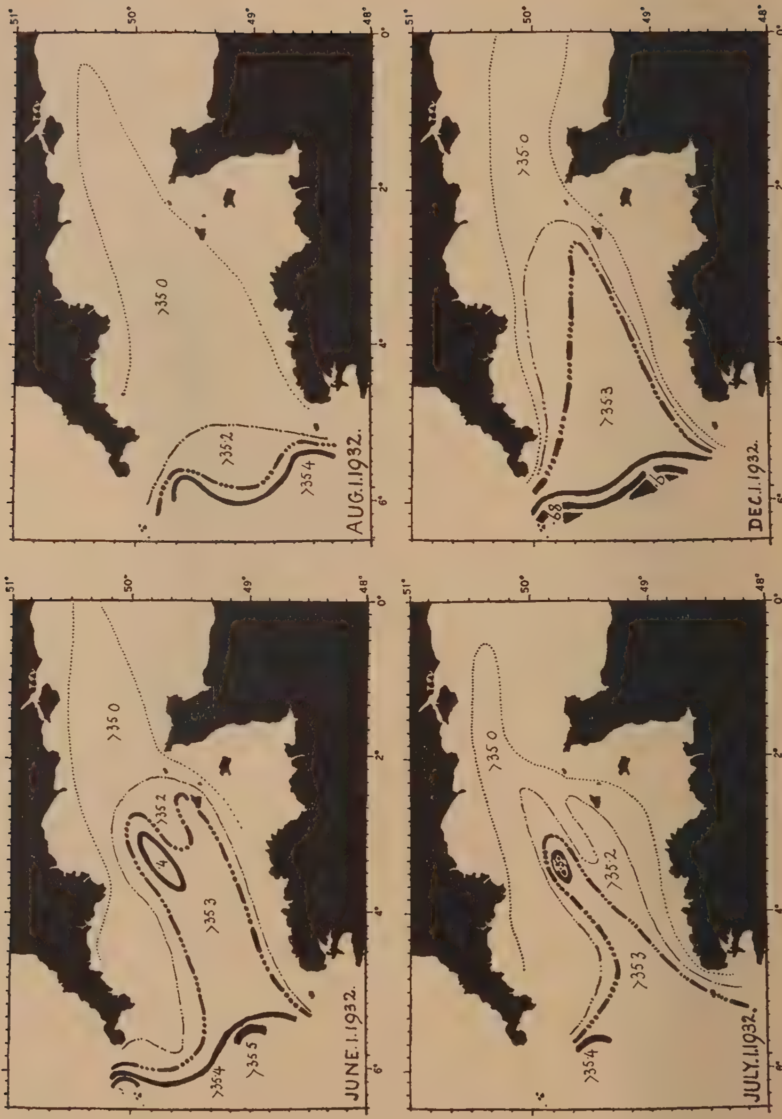
Fig. 6.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>35·4
JULY.1.1932.
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>35·2
>35·3
>35·4
DEC.1.1932.
>35·0
>35·3

Fig. 7.

The Variation of Excess Base with Depth in the English Channel with reference to the Seasonal Consumption of Calcium by Plankton.

By

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Assistant Chemist at the Plymouth Laboratory.

SINCE excess base or titration alkalinity increases with increasing chlorinity, the ratio, $\frac{\text{excess base}}{\text{chlorinity}}$, termed by Wattenberg the "specific alkalinity," is the most suitable quantity to consider when determining whether or not excess base varies with depth or from time to time. Wattenberg (**5**) has shown that a marked increase occurs in the great ocean depths immediately above the bottom. There is at present no evidence, other than that found by the writer (**2**), for the English Channel in the summer of 1931, to suggest any variation of excess base in shoal water on the continental shelf and away from the influence of large rivers such as appear to affect the Heligoland Bight (Zorell, **6**). The variation found in 1931 was small and of the order of the experimental error of any one pair of observations. To overcome this difficulty, statistical methods were applied to the grouped results obtained from similar depths during the summer and early autumn of 1931. The differences found between the specific alkalinities of the surface and bottom waters were several times the standard errors. The conclusions, however, were open to criticism in that the experimental results were not designed for statistical treatment.

In the summer of 1933 the problem was attacked somewhat differently. From each sample, contained in a number of 170 ml. standard sample bottles, about six to fifteen sub-samples, each 100 ml., were analysed for excess base by the method of Wattenberg (**4**) which had been used in 1931. It is generally recognised that in making a series of consecutive determinations on one quantity, the later results may not be independent of the earlier. Particularly in reading a burette there is a tendency to "adjust" the value read in accordance with the knowledge already gained on the sample. To overcome this, analyses of sub-samples of different samples were carried out in a haphazard sequence in flasks marked by a reference letter only, so that the origin of the sub-samples was at the time unknown. Again, in some analyses the volume of the sub-sample was increased by 1 ml. in order slightly to displace the titration.

The standardisation of the N/20 baryta in terms of 10 ml. of N/20 hydrochloric acid was carried out in quadruplicate and the mean taken as the true value. From this each titration of sea-water was subtracted in order to get the " baryta equivalents " of the excess base. These were then corrected for the error at the temperature of the laboratory of the two 100 ml. pipettes used for measuring the water. On each occasion the pipettes were calibrated by weighing the distilled water delivered under standard conditions. The distilled water had been allowed to attain the temperature of the laboratory and its volume was calculated from its temperature and weight. In any one working day the temperature of the laboratory did not vary by more than 2° C.

For each set of sub-samples, the mean baryta equivalent was found and the sum of the squares of the deviations from the mean gave the variance, $\Sigma\ d_n{}^2$. The standard error for the sample was then derived from the formula :—

$$\rho_A = \sqrt{\frac{\Sigma\ d_n{}^2}{n(n-1)}}$$

It must be admitted that owing to their small number the baryta equivalents of the sub-samples do not fall on a typical population curve. The means and standard errors were then multiplied by the baryta normality factor to give the excess base in milliequivalents per litre.

In earlier work the ratio considered for specific alkalinity, Λ, was :—

$$\Lambda_v = \frac{\text{excess base in milliequivalents per litre}}{\text{chlorinity in grams per kilogram}} = \frac{A_v}{Cl}$$

Elsewhere the writer (**3**) has discussed the advisability of replacing this volume/weight ratio by the weight/weight ratio :—

$$\Lambda_w = \frac{\text{excess base in milliequivalents per kilogram}}{\text{chlorinity in grams per kilogram}} = \frac{A_w}{Cl}$$

i.e. a ratio which varies with temperature may be replaced by one which is invariant. The excess base has therefore been converted to milliequivalents per kilogram by dividing by σ_t, the density found from the chlorinity and the temperature of the laboratory.

Since the determinations of chlorinity are relatively considerably more accurate than those of excess base, fewer sub-samples were called for. Indeed, no great error would be introduced by ignoring the standard error of the chlorinity and relying on one determination. The specific alkalinity has then to be found from the expression :—

$$\Lambda \pm \rho_A = \frac{A \pm \rho_A}{Cl \pm \rho_{Cl}}$$

TABLE I.

Date 1933 and temp. of Lab.	Station	Depth metres	EXCESS BASE				CHLORINITY			SPECIFIC ALKALINITY	
			No. of sub-samples analysed	Av (vol/wt) milli-equiv per litre	Aw (wt/wt) milli-equiv per kg.	Aw (wt/wt) Standard Error ρA_w	No. of sub-samples analysed	Cl ‰	Standard Error ρCl	$\Lambda_w \times 10^4$	Standard Error $\Lambda_w \times 10^4$
18/7 24°C	L 4	0	7	2.3692	2.3146	0.00207	6	19.323	0.0027	1197.8	1.19
		50	6	2.3850	2.3299	0.00277	6	19.341	0.0038	1204.7	1.45
	L 6	0	12	2.3590	2.3046	0.00178	4	19.314	0.0013	1193.3	0.93
		5	4	2.3623	2.3078	0.00349	3	19.322	0.0036	1194.4	1.82
		25	13	2.3724	2.3176	0.00148	5	19.350	0.0020	1197.7	0.78
		68	15	2.3814	2.3263	0.00242	4	19.359	0.0038	1201.7	1.27
10/8 22.5°C	E 1	0	5	2.3604	2.3051	0.00132	1	19.36	-	1190.5	0.70
		69	5	2.3690	2.3134	0.00498	1	19.33	-	1196.8	2.60
19/9 18°C	L 4	0	6	2.3582	2.3000	0.00107	4	19.379	0.0013	1186.8	0.56
		50	9	2.3740	2.3153	0.00235	4	19.390	0.0029	1194.1	1.22
	E 1	0	8	2.3617	2.3027	0.00286	3	19.434	0.0021	1184.9	1.47
		69	10	2.3768	2.3181	0.00136	3	19.417	0.0032	1193.8	0.73

The writer is indebted to Prof. R. A. Fisher for the following method of obtaining ρ_{Λ} from ρ_{A} and ρ_{Cl}.

$$\text{Let } \Lambda \pm \rho_{\Lambda} = \frac{A \pm \rho_{A}}{Cl \pm \rho_{Cl}} = \frac{A(1 \pm \xi_{A})}{Cl(1 \pm \xi_{Cl})}$$

Then since, for small variations, the relative variance of the quotient is equal to the sum of the relative variances of the numerator and denominator,

$$\therefore \quad \Lambda \pm \rho_{\Lambda} = \frac{A}{Cl}\left(1 \pm \sqrt{\xi_{A}^{2} + \xi_{Cl}^{2}}\right)$$

$$\therefore \quad \rho_{\Lambda} = \frac{A}{Cl}\sqrt{\xi_{A}^{2} + \xi_{Cl}^{2}}$$

In Table I are first given date, station, depth and the excess base in milliequivalents per litre, A_v, for comparison with earlier work. Then follow excess base in milliequivalents per kilogram, A_w, and chlorinity in grams per kilogram each with their standard error and the number of sub-samples. Finally is given the specific alkalinity, $\Lambda_w \times 10^4$.

Since the mean values and their standard errors are to be used for further statistical calculations, they are given to five significant figures. Although this is not usual in chemical work it is felt that the tests of significance in Table II are thereby rendered more precise.

TABLE II.

Variation of Specific Alkalinity with Depth.

Date 1933.	Station.	Depths compared metres.	Differences in $\Lambda_w \times 10^4$ with standard error.	Difference in Ca. mg./metric ton with standard error.	
18/7	L4	0 & 50	$+6{\cdot}9 \pm 1{\cdot}87$	$+270 \pm 70$	Significant.
	L6	0 & 68	$+8{\cdot}4 \pm 1{\cdot}57$	$+325 \pm 60$	Significant.
		0 & 25	$+4{\cdot}4 \pm 1{\cdot}21$	$+170 \pm 50$	Significant.
		5 & 25	$+3{\cdot}3 \pm 0{\cdot}80$	$+130 \pm 30$	Probably significant.
		25 & 68	$+4{\cdot}0 \pm 1{\cdot}49$	$+155 \pm 60$	Significant.
10/8	E1	0 & 69	$+6{\cdot}3 \pm 2{\cdot}69$	$+245 \pm 105$	Significant.
19/9	L4	0 & 50	$+7{\cdot}3 \pm 1{\cdot}34$	$+280 \pm 50$	Significant.
	E1	0 & 69	$+8{\cdot}9 \pm 1{\cdot}64$	$+345 \pm 65$	Significant.
Mean for all stations and dates.		Surface and bottom.	$+7{\cdot}6$	$+295$	

It will be seen that in all cases the specific alkalinity increases with depth. In Table II will be found the differences in specific alkalinity, $\Lambda_w \times 10^4$, between given pairs of depths. The standard error of the difference is derived from the expression :—

$$\rho_{\Lambda \text{ diff.}} = \sqrt{\rho_{\Lambda_1}^{2} + \rho_{\Lambda_2}^{2}}$$

These differences are all positive, that is, the specific alkalinity increased with depth. They are somewhat less than was found in 1931, but owing to the groups of analyses being made each on sub-samples of one sample the standard errors are much less.

There remains little doubt that the variations found in 1931 were real and that small variations in specific alkalinity do occur in the shallow waters of the English Channel.

As a result of Wattenberg's investigations (**5**) on board the *Meteor* in the South Atlantic, it would appear that these variations are in large part due to variations in calcium. According to his data the water in the English Channel is always slightly supersaturated with calcium carbonate (Table III). Since in summer the percentage supersaturation amounts to 30 or 40 per cent, the increase in calcium towards the bottom cannot be attributed to re-solution of bottom deposits ; rather must the water be regarded as in unstable equilibrium ready to deposit calcium carbonate on suitable nuclei of calcite (cf. Wattenberg's review of the literature of this subject, **5**).

TABLE III.

PERCENTAGE SATURATION OF CALCIUM AS CARBONATE WITHIN THE RANGE OF pH AND TEMPERATURE FOUND IN THE ENGLISH CHANNEL, (FROM DATA BY WATTENBERG, **5**, TABLE 31).

pH t, °C.	8·0	8·1	8·2	8·3
8°	110	115	121	128
12°	113	119	126	134
16°	117	124	132	140

The lower calcium content of the surface water can be explained by deposition of calcium carbonate in the skeletons of flagellates and calcareous algæ which afterwards die off, falling to the bottom, or are eaten, the calcium going to build up the skeletons of crustaceans and teleosts (see however p. 753).

The presence of calcium and other cations as chlorides in body fluids in concentrations similar to those in sea-water does not affect these calculations. In the main, depletion of calcium in the water may be attributed to its deposition as carbonate or phosphate in the skeletons. Magnesium, in so far as it is concerned in such deposition, is included with calcium for the purposes of this discussion.

The degree of accuracy necessary for the statistical treatment is relative and confined within any one batch of samples analysed at any one time. Analyses made at different times are affected by errors in the standardisation of the baryta by hydrochloric acid, of the hydrochloric acid by sodium carbonate and of any change in the latter standard. These have not been treated statistically. Thus summer determinations of specific alkalinity could not be compared in time with spring determinations even if these existed.

Nevertheless the data of July 18th, 1933, for Station L6 may be used for a very rough calculation of the production of calcareous plankton.

Let us suppose that the bottom layer of water (68 metres) had remained unchanged in its specific alkalinity, A_w, since the previous winter. The differences in A_w between this layer and the surface, 5-metre, and 25-metre layers are known (Table II), so that with the aid of the procedure outlined in (**1**), p. 723, it is possible to work out the total deficiency in A_w for the whole water column of 70 metres depth and one sq. metre cross-section.

$$\delta A_w \times 10^4 = \delta \frac{A_w}{Cl} \times 10^4 \; -212{\cdot}2$$

Regarding Cl as constant and equal to 19·4 g. per kg. or $19{\cdot}4 \times 10^3$ g. per metric ton,

$$\therefore \quad \delta A_w = \frac{19{\cdot}4 \times 10^3}{10^4} \times 212{\cdot}2 \text{ milliequivalents for the whole water column.}$$

For the present purpose the density of the sea-water may be taken as unity, so that $\delta A_w = \delta A_v$;

whence $\delta A_v = 410$ milliequivalents for a column 1 sq. metre in cross-section and 70 metres deep.

If the entire loss of excess base can be attributed to deposition of calcium in plant skeletons, this is equivalent to 8·2 g. Ca beneath each sq. metre or 8·2 metric tons beneath each sq. kilometre. The writer has been unable to find any quantitative data on the amount of calcium in the skeletons of calcareous phytoplankton, but if this is *assumed* to be 10% of the wet weight the production of calcareous algæ works out at 82 metric tons per sq. kilometre of surface. This figure may be compared with the total plankton crops calculated from changes in other constituents in (**2**), p. 744.

Basis.	Minimum production of phytoplankton wet weight, metric tons per sq. km.
CO_2	1,600
O_2	1,000
Phosphate . .	1,400*
Nitrate . . .	1,500
Silicate . . .	110
Calcium	82

* This figure is corrected from the original (1,200 tons) for the salt error in the determination of phosphate which was ignored.

As was stated in (2), p. 744, silica is of no use to animals feeding on diatoms and is probably excreted immediately into the sea-water where it may be quickly redissolved. If the intestinal juices of the zooplankton are alkaline it may even be excreted already in solution. In either case, the silica appears to take part in the life cycle several times in one season.

So far as calcium is concerned, the writer is not clear just how far zooplankton, such as, for example, Limacina and the larvæ of other molluscs, are dependent for calcium on their ingested food or how far they are able to absorb it directly from the sea-water across the body wall, but in either case the net result will be its removal from the water for the life of the animal or until the next moult.

Since a part of the calcium consumption may be attributable to direct assimilation by zooplankton without first passing through the stage of phytoplankton, the above calculation is strictly comparable neither with the silicate nor with the first four of the above nutrient salt data.

The writer is greatly indebted to Prof. R. A. Fisher of the Galton Laboratory, to whom the draft of the paper was submitted, for helpful criticism and advice. The following quotations are taken, with permission, from a letter of his dealing with the validity of the statistical treatment.

" . . . I think that, with the precautions you mention on page 2 (p. 747 of text), as to randomising the flasks in the laboratory, there can be no question of the validity of your conclusion. Reading to three figures, beginning with 5 is equivalent to admitting errors up to ±1 in 1000, or a standard error of observation of about 0·7 in 1200. The fact, however, that you have based each value on not less than four subsamples reduces this so to speak deliberate error to a half, or in some cases nearly to a quarter of this value. So that there is no theoretical impossibility in your finding, as you have done, differences of 6 or 8 units definitely significant."

Referring to the reporting of data to five significant figures, he says: " Personally I should like to see the five figures retained, as they make the tests of significance definitely more precise, but if it goes against the grain of chemical tradition to publish final figures, which are very unlikely to be exact for the material examined, it might be made clear that such a figure as 1193·3 with a standard error ±0·93 implies that the final figures lie between 1191·4 and 1195·2 with the rather high probability of about 20 to 1, but as among the numbers within this range the value printed, 1193·3, is only the most likely among a number of values of almost equal plausibility. In fact, if you were giving a guarantee, you would probably not take narrower limits than I have stated. But 1193·3 is definitely, though not greatly, more likely than 1193·0, just as at 68 metres 1201·7 is more likely than 1202·0, so that the test of significance appropriate to the comparison of these two most likely values is properly carried out on the difference 8·4, whereas the approximate difference 9·0 would be rather inaccurate for this purpose."

SUMMARY.

In the English Channel in summer a small difference in specific alkalinity between the surface and bottom waters has been established by a statistical method. This is not due to re-solution of bottom deposits of calcium carbonate with which the water is supersaturated. It is attributed to removal of calcium from the surface waters by plankton and an attempt has been made to calculate the production of calcareous plankton.

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The Determination of Phosphorus and Nitrogen in Plankton.

By

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DURING the course of an investigation on the seasonal changes in phytoplankton (Harvey, 1934), the need arose for analyses of organic phosphorus. The quantities available being very small it was necessary to develop a method of analysis.

Since the plankton consists of many different organisms ranging widely in size and shape and organic content, neither a description of its composition, its volume, nor its wet or dry weight gives a clear indication of its value as food for other animals. It was considered that its phosphorus or nitrogen content, as indicative of protein content, would best serve this purpose and allow comparison to be made between different samples of plankton.

DETERMINATION OF TOTAL PHOSPHORUS IN PLANKTON.

The method of Juday, Birge, Kemmerer, and Robinson for total phosphorus in lake residues as modified by Robinson and Kemmerer (1930) and Titus and Meloche (1931), in which the plankton sample was digested with a mixture of sulphuric, hydrochloric, and nitric acids, was not satisfactory for marine plankton. It proved very difficult to drive off the last of the oxidising agent, which interfered with the subsequent reduction of the phosphomolybdate by stannous chloride. Various modifications of the nitric acid oxidation as well as a number of ignition methods were tried with only partial success. Finally perhydrol (Merck's 30% hydrogen peroxide) in presence of sulphuric acid was found to be the most suitable oxidising agent. For the determination of total phosphorus in sea-water Kreps and Osadchih (1933) used 3% hydrogen peroxide in order to oxidise and hydrolyse the organic matter, and Kalle (1933) for the same purpose used potassium persulphate whose action is essentially the same. Perhydrol has obvious advantages over weaker solutions of hydrogen peroxide. But, when the product of digestion was diluted to 100 ml. and treated with the usual molybdimetric reagents, the colour developed was invariably off shade. Furthermore, halogens set free by the oxidation of sea salts were only driven off completely when attention had been given to the design of an air bath which would enable the fumes to escape from the flask without collecting on its upper walls and running back. The following procedure has proved highly satisfactory.

Method. A suitable volume of the plankton concentrated in a small volume of sea-water, as obtained in the bucket of a tow-net, was filtered through a small disc of bolting silk (200 mesh to the linear inch ; Harvey, this Journal, pp. 770). The first 20–25 ml. of filtrate was again passed through the filter, since it was found to contain some of the smaller plankton organisms. The final filtrate, which was usually clear to the eye, was transferred to a small wash-bottle and used for washing down the sides of the funnel. The filter disc was removed from the funnel and the plankton washed into a 50 ml. Erlenmeyer flask with a jet of distilled water amounting to about 5–10 ml. in all. Concentrated sulphuric acid (0·2 ml.) was added and the liquid was evaporated without boiling during the course of one hour in a covered air bath at 115–120°, and subsequently slowly raised to 160°.

The carbonaceous residue in the flask at 150–160° was treated with Merck's perhydrol, drop by drop. By twirling the flask the perhydrol can be readily spread over the bottom of the flask before decomposing and three to five drops usually sufficed to oxidise the carbonaceous matter. It was found better to re-heat between successive additions of perhydrol. Occasionally the residue remained brown and in such a case it was taken up with 5 ml. of water, re-evaporated, and again treated with perhydrol. Five drops of perhydrol contained only $0{\cdot}1\gamma$ P_2O_5 which could be safely ignored.* Finally the flask was heated for twenty minutes at 180°. After cooling, about 8 ml. of distilled water was added and the solution allowed to simmer gently while the volume fell to about 4 ml. This treatment should have destroyed any persulphate which had survived heating at 180°. It is doubtful if it was of any value, as is sometimes claimed, in hydrolysing to orthophosphate any pyrophosphate which might have been formed [cf. Berthelot and André (1896)]. The good agreement between duplicate determinations and the recovery from trial runs with known amounts of phosphate showed that pyrophosphate was not formed. This agrees with the findings of Titus and Meloche (1931).

In order to remove silica, the acid solution was transferred to a calibrated 10 ml. pointed centrifuge tube and the Erlenmeyer flask washed out with 2 3 ml. of water in all. The acid solutions and washings were thoroughly mixed by a glass rod, their volume noted and centrifuged. Then 5 ml. of the supernatant liquor was pipetted off and made up to 100 ml. Aliquot parts of this were again diluted to 100 ml. and then compared in Hehner cylinders in duplicate with a standard containing, say, 12·5 γ P_2O_5 per 100 ml.* (=125 mg. P_2O_5 per cubic metre).

By this double dilution four advantages were gained : (*a*) the foreign matter which earlier upset the colour match was rendered innocuous, (*b*) when adding the acid molybdate reagent it was unnecessary to allow for the small excess of acid already present, (*c*) the salt error was made negligible, (*d*) two or more determinations could be made on the same digest. A set of analyses on three sub-samples of one sample of plankton is shown in Table I.

TABLE I.

ANALYSES IN TRIPLICATE ON MIXED PLANKTON FILTERED FROM 388 LITRES OF WATER AT STATION L4, BETWEEN THE SURFACE AND 45 METRES ON 12TH FEBRUARY, 1934.

Analysed on 13th and 14th February. Sub-samples each compared colorimetrically in duplicate.

Sub sample.	Phosphorus in Plankton expressed as γ P_2O_5 per cubic metre of sea-water, i.e. as parts per million million.
A	241
	230
B	246
	249
C	244
	245
Mean	242

The reducing agent consisted of a solution of about 0·1 g. of stannous chloride (clear crystals) in 10 ml. of concentrated hydrochloric acid. Two drops of this solution were added to the standard or sample under comparison, which was well shaken before and after adding quickly 2·0 ml. of the usual 2·5% solution of ammonium molybdate in 37·5% (by volume) sulphuric acid. This reversal of the usual order of addition of the two reagents has been found to give more consistent results.

Only one opportunity has presented itself of applying the method, as finally developed, to a catch consisting almost only of plants. The result is shown in Table II, together with a further analysis of a clean sample judged to consist of 70% to 80% plants and 30% to 20% animals. After making allowance for this, the quantity of organic phosphorus works out in both cases at about 0·3 mg. P_2O_5 per 1000 " units of plant pigments " (p. 771). This approximate ratio has already found application (p. 782), and its magnitude has been confirmed by a number of other analyses which have been made in connexion with a research now in progress.

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* $1\gamma = 0{\cdot}001$ mg. ; thus 1γ per litre = 1 mg. per cubic metre.

TABLE II.

Analyses of Plankton from which the Larger Organisms had been removed.

Date.	Description.	Phosphorus expressed as mg. P_2O_5 per litre of catch.	mg. P_2O_5 per 1000 " units of plant pigments " (p. 771) present.
1/1/34	Almost wholly diatoms	0·089	0·31
7/2/34	70% to 80% diatoms	1·47	0·27 to 0·31*

Determination of Total Nitrogen in Plankton.

The standard micro-Kjeldahl method of Parnas and Wagner, as described by Pregl (1930), has proved excellent. When using 5 ml. of N/100 hydrochloric acid to absorb the ammonia liberated, the amount of nitrogen in the sample needs to be between 0·15 and 0·6 mg. Thus about two to three times as much plankton is required as for the phosphorus determination. The plankton sample was washed straight off the silk disc into a micro-Kjeldahl digestion flask and 0·2 ml. of concentrated sulphuric acid added to avoid loss of nitrogen bases during the evaporation of the water. Most of this was removed by boiling off on the Kjeldahl heating stand and the evaporation completed in an air bath or oven at 120°. The digestion with sulphuric acid (1 ml.), mixed potassium and copper sulphates and perhydrol, and the distillation and collection of the ammonia in N/100 hydrochloric acid were carried out exactly as described by Pregl. Duplicate runs on a sample of tow-net plankton gave 1·47 and 1·52 mg. nitrogen per litre of sample, being 2·75 times the quantity of P_2O_5. This ratio is of interest because previous work at Plymouth has shown that the vegetation utilises two and a half times more nitrate-nitrogen than P_2O_5.

In subsequent work time was saved by adding immediately all the sulphuric acid (1 ml.) and the mixed sulphates to the plankton and wash water in the Kjeldahl flask. Evaporation of the water without bumping was assisted by adding occasionally a drop of perhydrol.

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* After deducting 30% to 20% for phosphorus present in animals.

SUMMARY.

Phosphorus in plankton has been determined by digestion with sulphuric acid and perhydrol followed by colorimetric determination.

Nitrogen has been readily determined by the micro-Kjeldahl method of Parnas and Wagner.

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Measurement of Phytoplankton Population.

By

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Hydrographer at the Plymouth Laboratory.

With 9 Figures in the Text.

It is known that the unicellular plants in the sea are not evenly distributed; not only do quantity and species change on proceeding away from the shore, but more or less extensive fields of some one species or community may be met with in the open seas.

The only strictly quantitative method of sampling the population is to centrifuge a small sample of water and count the plants in it. The amount of sea-water sampled is small, the time consumed in making the count is great, and the resulting list of species and their numbers per litre of water is difficult to interpret in terms of the crop. The species are so different in size and shape and quantity of contained organic matter, that a comparison of such lists of species does not give a clear picture of the relative proportion of vegetable organic matter in the waters. In considering the productivity of the sea, it is the quantity of vegetable food available for the animals rather than the number and kind of individual plants which is of primary interest.

It was the aim of this investigation to devise a rapid method of obtaining a measure of the quantity of vegetable matter in the water so that a number of estimations could be carried out over an area in a limited time. It seemed impracticable to separate the vegetable from the animal plankton, which ruled out any estimation of organic matter. The quantity of green vegetable pigments on the other hand is easy to estimate quickly, and gives a measure of the organic vegetable matter in mixed plankton. It is not supposed that the ratio of pigments to organic matter is constant either for any one species or for different species, but this ratio is probably a great deal more constant than the quantity of organic matter to size of cell and so gives as good a measure of the crop as counting and judging the amount of cell contents under a microscope. Pigment content as a measure of quantities of diatoms was first used by Kreps (1930).

Since it was impracticable to centrifuge sufficiently large samples of water, particularly during the barren months, the finest obtainable bolting silk—200 meshes to the linear inch—was used. This does let through the smallest phytoplankton organisms. Although these may at times be numerous, it is assumed that they do not make up any material proportion of the *volume* of the catch, except in low latitudes and possibly during the height of the summer when the quantity of diatoms is very small. It is also likely that a moiety of any *Skeltonema costatum* would be lost, as would some other small diatoms.

A water meter was constructed and attached as shown in Figure 1 to a net of bolting silk. The gear is drawn through the sea either up and down vertically, obliquely, or hauled horizontally. The water meter measures the volume of sea-water which passes into the net and is filtered through it. The use of a water meter in the mouth of a tow-net had been suggested by Nansen (1915) and a net with meter to measure the water which had actually passed through it was constructed by Dr. E. J. Allen and exhibited at a meeting of the Challenger Society. However, I can find no record of a measuring net having been used to any extent.

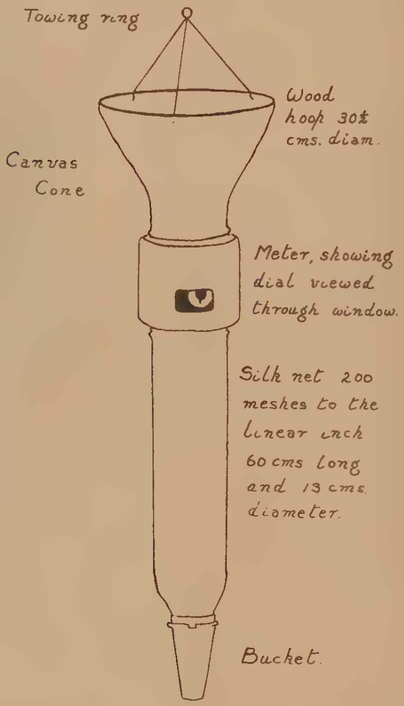
Towing ring
Wood hoop 30½ cms. diam.
Canvas Cone
Meter, showing dial viewed through window.
Silk net 200 meshes to the linear inch 60 cms long and 13 cms. diameter.
Bucket.

FIG. 1.—Diagram of the measuring net.

The catch is washed into the bucket, its volume measured if it is desired to keep a small aliquot portion for examination and counting, and the rest filtered through a disc of bolting silk about 3½ cm. in diameter. This disc is put into a tube with a few c.c. of 80% acetone which dissolves the yellow-green pigments from the phytoplankton. The quantity of pigment is then estimated by comparing this known volume of acetone solution with colour standards.

The Meter.

The meter is shown in Figures 2 and 3. The rotor consists of a brass spindle revolving freely on agate cups and points. On this a small brass boss 6·5 mm. in diameter is mounted, into which are screwed and soldered six short arms of hard brass wire, 1·7 mm. diameter, to which are soldered vanes of brass foil 0·25 mm. thick, the soldered joint being kept coated with cellulose enamel. A worm gear is cut in the after end of the spindle. It is essential that the rotor be carefully balanced, and this was done by filing from some vanes, adding very small amounts of solder to others, until it revolved quite regularly when drawn very slowly through water and did not tend to stop in any one position.

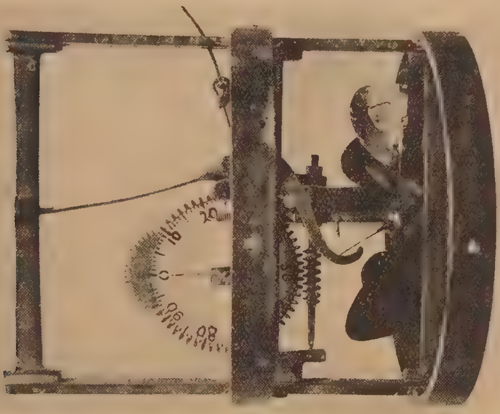

Fig. 2.—Photograph of meter removed from outer casing. The spring arm and cord which stops the rotor revolving is shown.

The shaft carries a pinion wheel having ten teeth which engage with the worm gear on the spindle of the rotor. On the other end of the shaft a second worm gear is cut, and engages with the 60-toothed dial wheel, which is enamelled white on one face with 100 divisions marked in black, every tenth division being numbered. Mounted behind the dial wheel and engaging with a pinion wheel attached to it, a second toothed wheel makes one revolution for every four revolutions of the dial. Quantities up to 4½ cubic metres of water can in this way be recorded.

Calibration of the meter.

The meter in its case was mounted on a partition in a trough through which water was passed in a steady stream (Fig. 4). In order to eliminate air bubbles and reduce swirls the water was led into a preliminary compartment as shown in the figure. After trials in this laboratory, the meter described was calibrated at the National Physical Laboratory, where a larger flow of water and means of accurate measurement were obtainable. The results of this calibration are shown in the following table :—

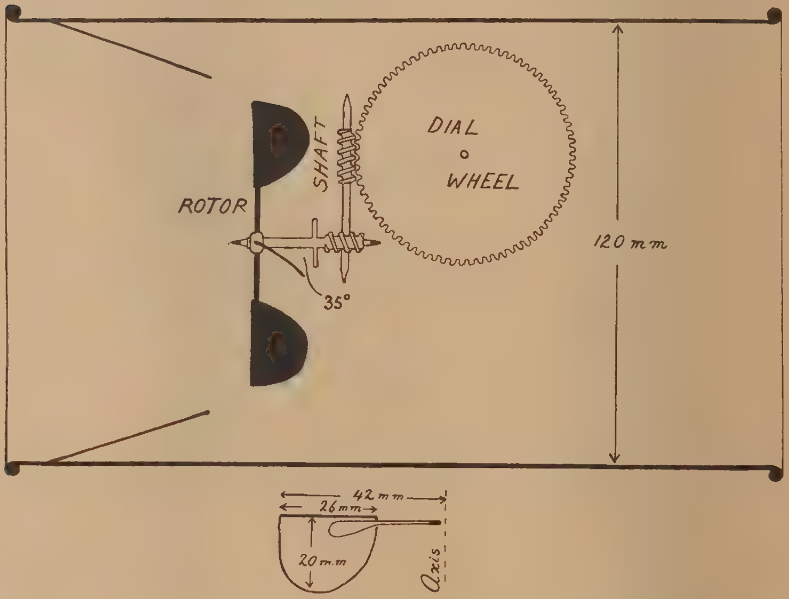

Fig. 3.—Sectional diagram showing meter in outer brass case, and details of vane.

Rate of passage of water through the meter.	Litres of water passed for every unit division on the dial wheel.
47 litres per minute	12·20
79 ,, ,, ,,	11·60
148 ,, ,, ,,	11·40
550 ,, ,, ,,	12.20

For practical purposes it is taken that the passage of 12 litres of water registers one division on the dial, provided the rate of flow lies between 47 and 550 litres per minute. If the net were very heavily clogged, the passage of too little water would be recorded during the latter part of the haul; thus an extraordinarily rich plankton might appear somewhat richer than it really was. Such conditions have not yet been met with.

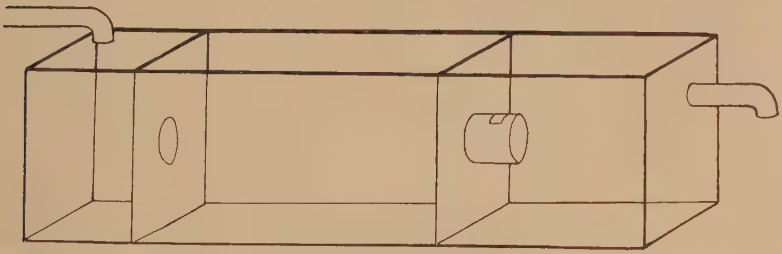

Fig. 4.—Diagram of tank used for calibrating the meter which is shown mounted on the right-hand partition.

As ordinarily fished while making vertical hauls some 120 to 200 litres of water per minute pass through the net.

When the measuring net is drawn out of the sea, and when being lowered on a windy day, the rotor will spin. This necessitates the provision of a stop or brake, which is released when the net is in the water and engaged again before it is drawn out of the water. The photograph shows the spring arm used for this purpose. On pulling the light cord attached to it, it engages with a brass pin mounted on the spindle of the rotor, and on being released it flies back, allowing the rotor to turn.

The Measuring Net and Gear.

The general arrangement as used when fishing from a boat is shown in Figure 1. The ring on the three wires holding the hoop is attached to a line about 2 metres above a lead. In order that the net may fish equally well when being lowered, hauled up or towed the brass case is surrounded by a wooden jacket so that the meter has but little positive or negative buoyancy when immersed in water.

In order that diatoms caught up at the joint between the silk net and bucket may be washed out into the bucket, the following construction is employed.

The bottom of the silk net (7½ cm. diameter) is slipped over a brass carrier (Fig. 5) and held by a thin rubber band. A brass band is placed over this as shown in the sketch and screwed up tight. A rubber washer and brass foil washer are attached to the carrier. The brass bucket is pushed against this and by means of a twist held firmly by the four cams. The brass bucket and carrier do not exceed 400 gm. in weight.

From a boat, where one can reach over and release the brake or stop when the meter is in the water and engage it again before drawing the net out of the sea, this arrangement is simple to work. A haul to 40 metres depth may be completed and the contents of the bucket emptied into a jar or a filter in about 4 minutes. However, from a ship, except in very calm weather, the net may twist round the wire or may go down with air entrapped in it. In the earlier work the brake or stop was actuated by means of a " Bowden wire," but a more satisfactory arrangement was finally devised, which not only enables the net to be used in moderate weather provided the ship is not rolling unduly and putting too great a strain on the gear, but also allows vertical hauls to be made between any two desired depths, or horizontal hauls at any desired depth.

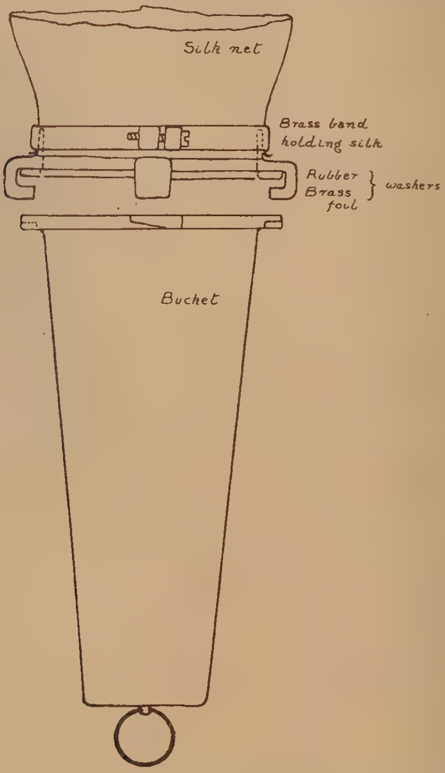

Fig. 5.—Drawing of bucket and attachment to the silk net.

THE THROTTLING GEAR.

The measuring net is lowered with the canvas mouth throttled and a strain on the line actuating the brake or stop. The net is held as shown in Figure 6, A, by means of a wooden frame attached to the meter.

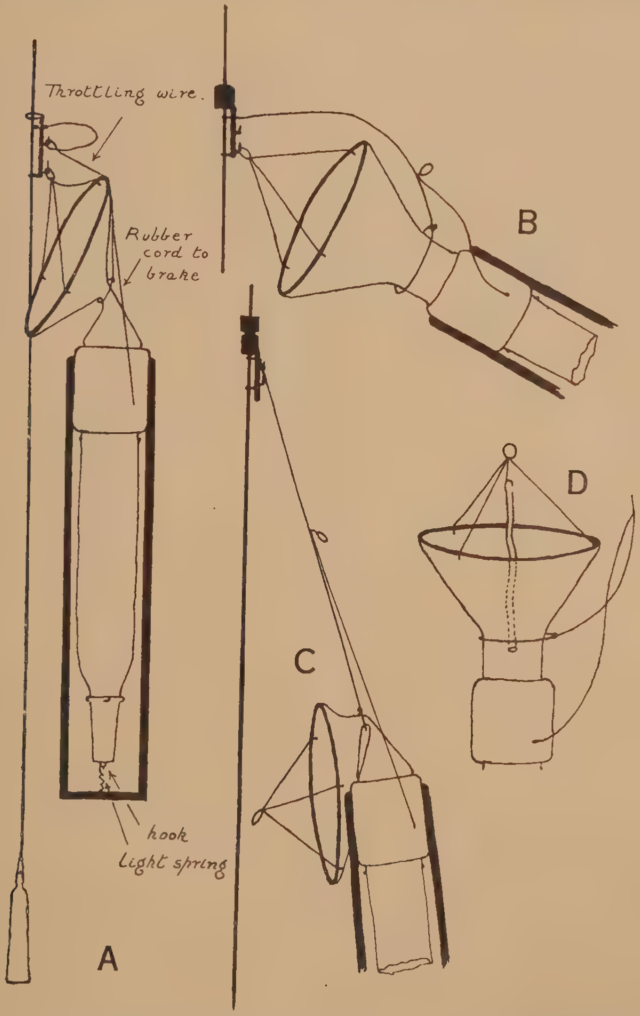
Throttling wire.
Rubber cord to brake
hook
Light spring
A
B
C
D

FIG. 6.—Diagram of throttling gear. A, shows net being lowered from ship. B, shows the net fishing after impact of first messenger. C, shows net throttled after impact of second messenger and ready to haul on board.

When the gear has been lowered to the desired depth, a messenger is sent down the wire. This actuates the first release, lets go the throttling line and slacks off the rubber cord attached to the brake. The net then fishes (Fig. 6, B). When it is desired to throttle and haul the net, a second messenger is sent down the line. This releases the ring attached to the wires holding the hoop of the canvas cone, throttles the net and again puts a strain on the brake (Fig. 6, C). The throttling wire is made of extra flexible steel wire $3\frac{1}{2}$ mm. diameter, the rubber cord of "lingerie elastic," the wooden frame of oak $2{\cdot}5 \times 1{\cdot}4$ cm. section, the canvas cone of light duck with a wooden hoop $1{\cdot}5 \times 1{\cdot}2$ cm. section. In order to hasten the escape of air as the apparatus is being lowered into the sea, a short piece of flexible metallic tubing 1 cm. diameter is attached inside the cone, as shown in Figure 6, D.

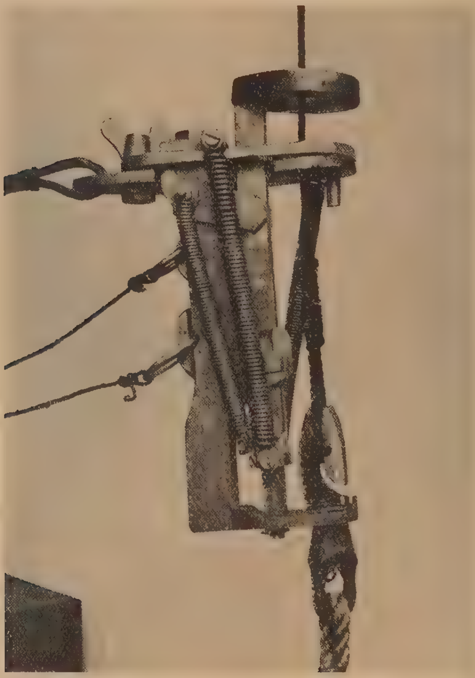

FIG. 7.

The double release is shown in the photograph (Fig. 7) and the principle on which it works in Figure 8. The impact of the first messenger knocks the slide down until it is stopped by the trigger hitting the body of the mechanism (B). A steel ring to which the throttling wire is attached is left free to fall out. Two brass springs, one on each side of the slide, cause it to rise to the upper limit of its travel (C) when the trigger, freed from its guide, is pulled out by a third spring. The impact of a second messenger knocks the slide down to the lower limit of its travel, allowing the second steel ring, to which the canvas cone is attached, to fall out. An attachment to the trigger does not allow the first release ring to be

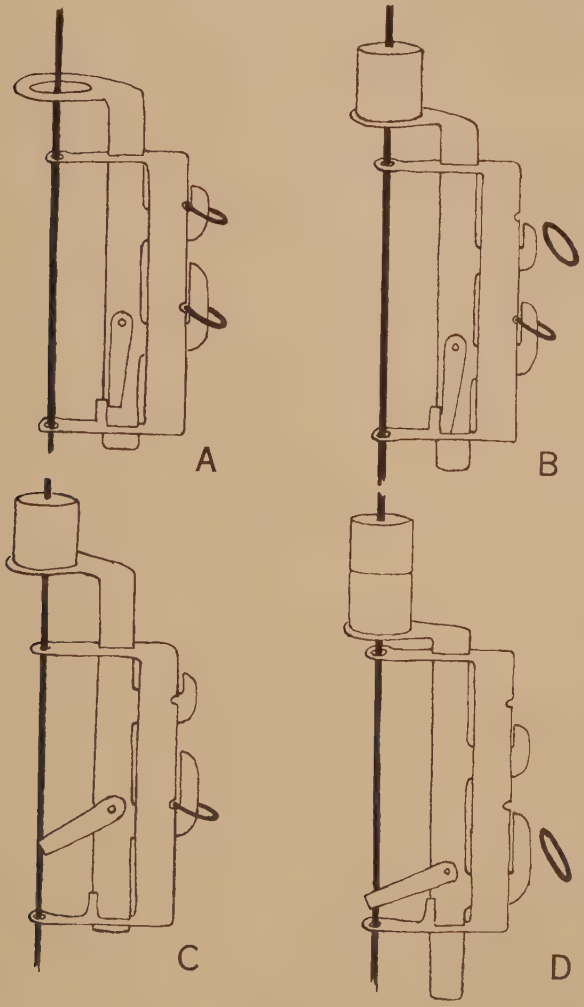

FIG. 8.

put in position unless the trigger is in the up and down position, engaged against its guide. The mechanism is attached to the wire hauling line, and is free to swivel round it. A lead of about 14 lb. is made fast to about 2 metres of light rope, the other end of which is spliced to the swivel on the mechanism.

THE FILTER AND COLOUR STANDARDS.

The catch is washed into the bucket and somewhat reduced in volume by shaking up into the net. The contents of the bucket, or a proportionate part, is passed through a small disc of bolting silk having the same mesh as the net –200 strands to the linear inch. A convenient apparatus is shown in Figure 9, where the silk disc rests on fine metal gauze to reduce any strain on it. As soon as the water has run through, the silk with the wad of wet plankton on it is put into a glass specimen tube (17 mm. diameter) and covered with 80% acetone. Within a few minutes the yellow-green pigment of the plants dissolves, although it is reasonable to allow several hours for complete solution, and necessary in the case of Thalassiosira. If necessary more acetone is then added to reduce the colour to a pale green of such a depth that slight differences in intensity are most readily seen.

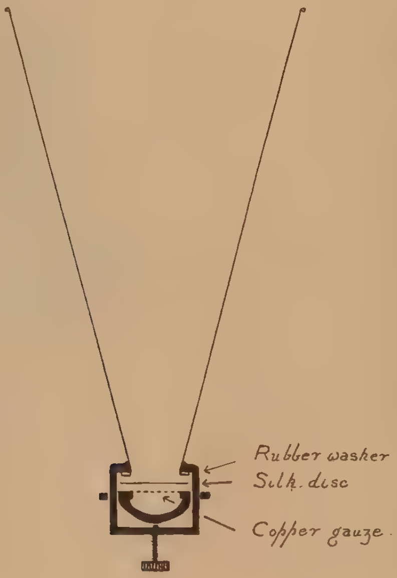

FIG. 9.

It is obvious that the colour comparison may be made in a variety of ways. The use of a spectrophotometer with monochromatic light of wave length within a chlorophyll absorption band would doubtless give the most accurate index. Actually the following very simple technique was employed and found satisfactory unless there were many pigmented copepods and larvæ in the catch, and the diatoms were not abundant. Under these circumstances the values obtained were probably too high.

A green solution was prepared, being an almost exact visual colour match with an acetone extract of diatoms. At first a mixture of chromate and chromium salt was used, later a mixture of potassium chromate and nickel sulphate was found more suitable. A solution in distilled water, made faintly acid, containing 25×10^{-6} gm. potassium chromate and 430×10^{-6} gm. nickel sulphate—$NiSO_4$, $6H_2O$—was taken as containing one arbitrary "unit of colour or pigment." A series of specimen tubes, all 17 mm. diameter and stoppered with waxed corks, were filled with concentrations of this mixture containing respectively 2, 4, 5, 6, 8, 9, 10, 12, 14, 16, and 19 "units of pigment per c.c." If the acetone extract of the catch was more coloured than the tube containing 14 "units of pigment" per c.c., it was further diluted to fall within the range of 8–12, the volume of extract measured and the colour comparison made. The method of calculating and expressing the results is shown in the following example: 550 litres of water had been filtered through the net, the dial of the meter having travelled through 46 divisions. The acetone extract measured 9·3 c.c. and matched the standard tube containing 8 units of pigment per c.c. Hence the acetone extract from the phytoplankton in one cubic metre of water would contain $\frac{1000}{550} \times 8 \times 9{\cdot}3$ "units of pigment." The results are thus expressed in units of plant pigments per cubic metre of sea-water.

During the first year's working with this measuring net, and the earlier models which led up to it, it was noticed that materially more water passed through the net when it was dry to start with than when it had been in use and wet for an hour or more. Further, a slight drift of the ship while a vertical haul was being made caused an unexpectedly larger quantity of water to pass through the net. These observations suggest that vertical hauls without the use of a meter do not necessarily give comparable results.

Irregular Distribution of Phytoplankton Organisms.

A series of vertical hauls to the same depth at or near the same position, that is to say through materially the same body of water, show that the diatoms are not distributed evenly. The following values were obtained near the same position, 5 miles south-west of Plymouth Breakwater.

	Hauls to 20 metres depth.	Hauls to 40 metres depth.	Hauls to 50 metres depth.	
Units of pigment	3800		4800	May 22, 1933.
per cubic metre	2600		4730	
	2850		5180	
	3500		4400	
	3080		5500	
	2280		3500	
	2380		3730	
	2530	Max. deviation 21% from mean.		
Max. deviation 32% from mean				
	less than 50	6400		June 28.
	,, ,, 200	4100		
	300	1280		July 17.
	395	1250		
	1000	940		Oct. 25.
	1310	1260		
		1230		
		1130		
		1380		
	3200			Nov. 23.
	4100			
	3100			
	3850			
	3500			
	2900			
	3540			
	2400			
	3300			
	3100			
	2500			
	3000			
Mean	3200	Max. deviation 25% from mean.		

Although these differences are considerable, particularly during the summer, even if a solitary observation should differ grossly from the mean, it does not obliterate the general picture of crop distribution which is given by this method, the differences in crop from place to place and from time to time being so great.

CORRELATION OF THE "UNIT" OF PLANT PIGMENTS.

During May catches of *Rhizosolenia alata* were obtained, almost free from other diatoms. Counts were made of the number of this diatom per c.c. of catch, and a measured volume filtered and extracted with acetone. A similar assay was made with a culture of *Biddulphia regia*,* in a healthy condition growing in Allen–Miquel enriched sea-water. These showed that one "unit of pigment" was dissolved from

6950 7300	individual cells of *Rhizosolenia alata*, a small form.
224	,, ,, *Biddulphia regia.*

SUMMARY.

A meter is described which measures the volume of water which has passed through a silk net which may be either towed or lowered and raised vertically.

A double release gear and throttling arrangement allows the net to be opened and, later, closed at any desired depths.

The catch of phytoplankton, from a volume of water which has been measured by the meter, may be assessed from its content of yellow-green pigments, which readily dissolve in acetone.

A rapid method of measuring the pigment content of the catch in terms of arbitrary units of plant pigment is described. The arbitrary unit is related to numbers of two species of diatoms.

The irregular distribution of phytoplankton in the sea is considered in connexion with representative sampling with this measuring net.

REFERENCE.

KREPS, E., and VERBINSKAYA, N. 1930. Seasonal Changes in the Barents Sea. Journ. de Conseil, Vol. 5, pp. 327–345.

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* For this I am indebted to Miss P. Jenkin.

Annual Variation of Planktonic Vegetation, 1933.

By

H. W. Harvey, M.A.,
Hydrographer at the Plymouth Laboratory.

With 5 Figures in the Text.

Since February, 1933, quantitative hauls have been made at frequent intervals with the measuring net previously described in this Journal, Vol. XIX, pp. 761–773, at the entrance to Plymouth Sound and seaward thereof. The more usual positions are shown in the sketch chart, Figure 1. On passing out of Plymouth Sound the salinity of the water increases more or less rapidly, according to the state of the tide and flow from the rivers, until near the position L_3, after which the increase is gradual. In winter or after heavy weather the water becomes noticeably more transparent in the neighbourhood of L_3.

Although the water at L_4, three miles beyond L_3, is not beyond the immediate influence of the land, it would seem that more or less open sea conditions are reached there. Observations made up to 15 miles farther seaward in March, April, and May showed that the phytoplankton did not remain the same either in composition or abundance, but suggested that observations at L_4 gave a measure of conditions farther to seaward. For this reason, and because it is accessible by motor boat during fine weather, most of the observations of this preliminary first year's survey were made at L_4 and the inshore positions.

In most cases the net was lowered twice to 20 metres depth or once to 40 metres, during which operation it filtered between 200 and 350 litres of water, according to the drift of the ship and the length of time the net had been in use. A small portion of the catch was usually reserved to examine the nature of the plankton, and to note the dominant species of plants. The remainder was used to estimate " units of plant pigment " per cubic metre of water filtered (p. 771). The vertical sections, Figures 2, 3, and 4, show the changing density of population on passing away from the shore and the rapid changes which take place in quite short intervals of time, which are also shown in Figure 5. The values shown in Figures 2, 3, 4 are in many cases the average of a number of observations.

Many of the lesser changes which take place are doubtless due to the mass of water which occupied the area having moved away to be replaced by other water, bringing its own flora with it. The incoming water is usually of similar salinity and has previously occupied similar areas. Any big change in the flora brought in with a new water mass would indicate that the new water came from an area having different conditions for plant growth, and it is therefore probable that such a change would be accompanied by a considerable change in salinity. Provided no marked salinity changes take place it seems justifiable to consider the area as a closed one for the purpose of describing the seasonal changes in plant life within it, although we know that water may be frequently replaced by water of similar history, but the possibility has to be borne in mind that a

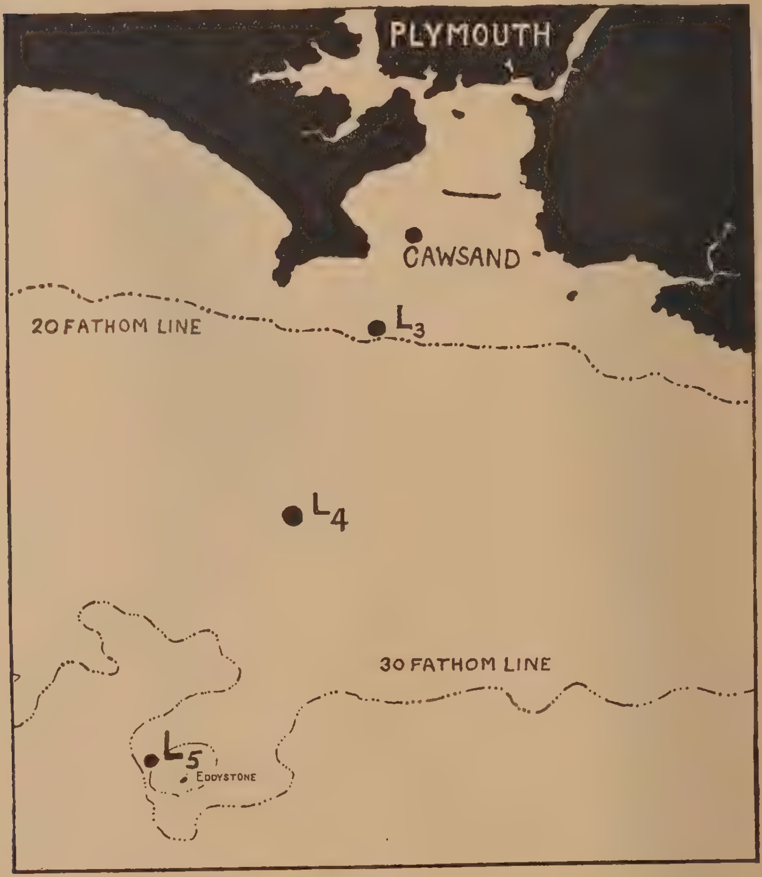


FIG. 1.

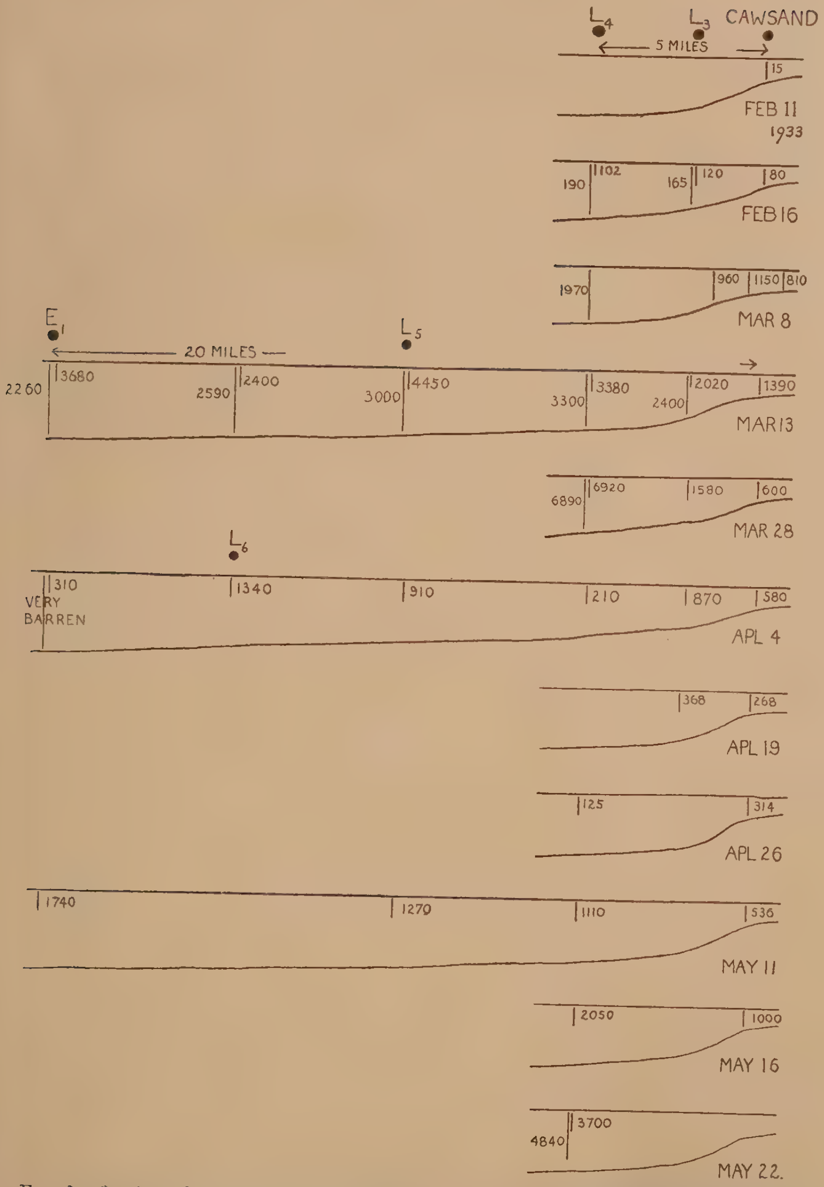
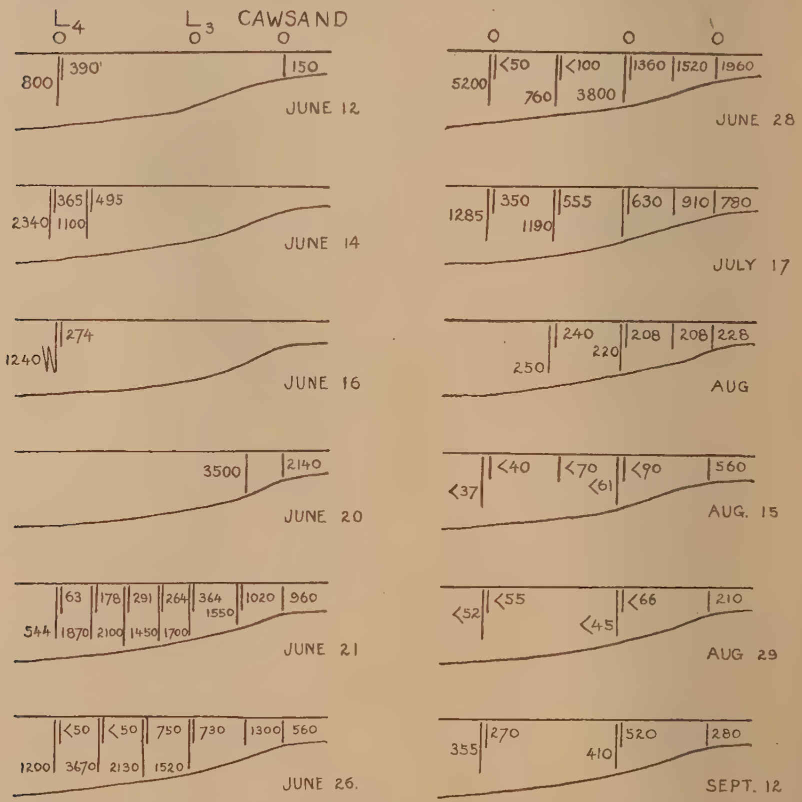


Fig. 2.—Sections showing the plant pigments in the catches, expressed as units of plant pigments per cubic metre of water filtered. The vertical lines indicate the depth to which the vertical hauls were made. In many cases the values shown are the mean value obtained from a number of vertical hauls.

mass of water which has had a very different history may move in, unheralded by any big change in salinity.

THE SPRING DIATOM OUTBURST, 1933.

The earliest observations at the beginning of February showed a very barren condition close inshore; on February 11th in Cawsand Bay only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L3
CAWSAND
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63
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178
2100
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264
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960
JUNE 21
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JUNE 26.
5200
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JUNE 28
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SEPT. 12

FIG. 3.—Sections showing the plant pigments in the catches, expressed as units of plant pigments per cubic metre of water filtered. The vertical lines indicate the depth to which the vertical hauls were made. In many cases the values shown are the mean value obtained from a number of vertical hauls.

about 15 'units of plant pigments' per m.³ were found. After five days with a daily average of 5 hours of sunshine, on February 16th, a series of horizontal and oblique hauls were made farther to seaward, the results of which are expressed in Figure 2.

On March 8th, after 20 lengthening days with an average of 3·8 hours of sunshine daily, a series of vertical hauls showed a tenfold increase since February 16th.

The observations on March 13th after a further five days of sunny weather showed further increase, and a similar density of population extending 15 miles to seaward beyond the position L_4. The flora was very mixed, many species of diatoms being present. Counts were made, but they only serve to give a general idea of the composition of the catch

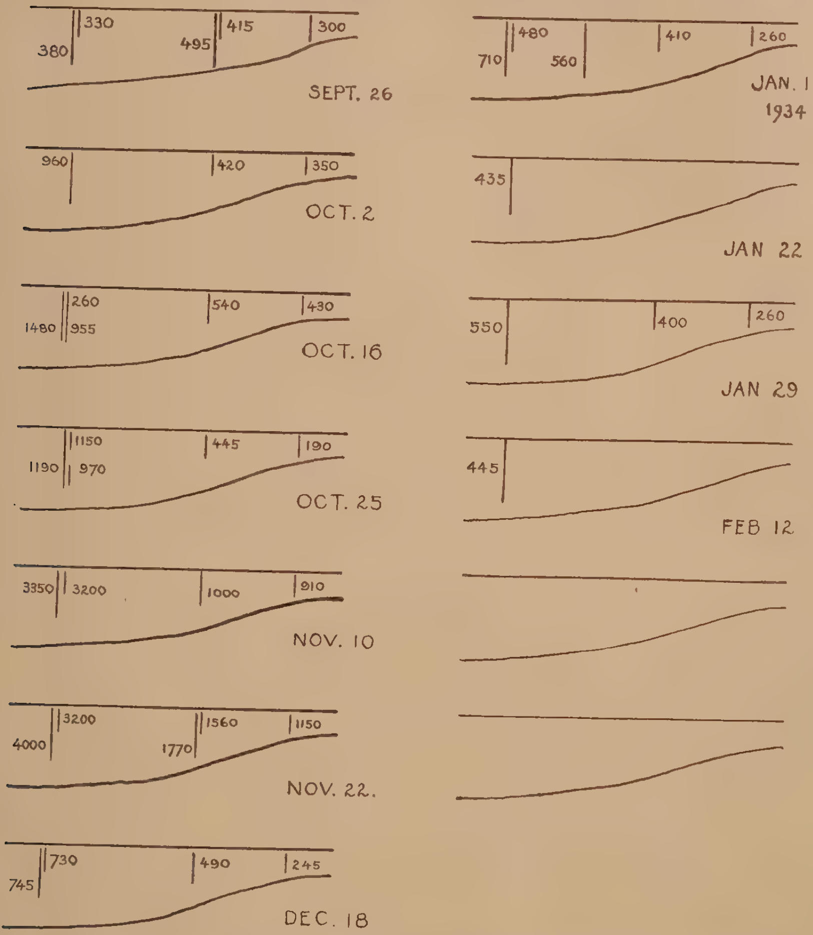

FIG. 4.—Sections showing the plant pigments in the catches, expressed as units of plant pigments per cubic metre of water filtered. The vertical lines indicate the depth to which the vertical hauls were made. In many cases the values shown are the mean value obtained from a number of vertical hauls.

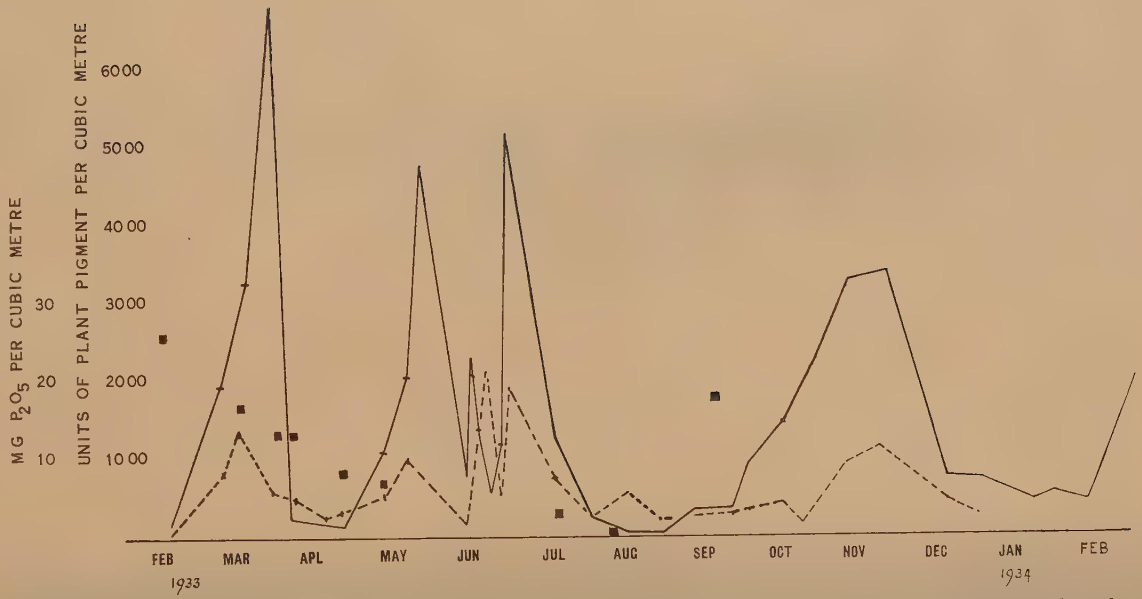

FIG. 5.—Diagram showing the mean content of plant pigments in the column of water at Station L_4 (plain line) and at the inshore station (pecked line). The black squares show the phosphate content of the column of water between surface and bottom at Station L_4.

because too few cells were counted. In fact, it was later concluded that such counts were likely to be misleading unless the diatoms in many fields under the microscope were counted and numbered in all 500 or more. This was not done except on a few occasions where it was desired to link up the pigment content with the number of individual cells. The following table only provides a general indication of the composition of the catches.

TABLE I.

Number of Individual Cells per Litre, March 13th, 1933.

	In vertical haul to 60-m. depth at E_1.	In vertical haul to 45-m. depth at L_4.	In vertical haul off Cawsand.
Biddulphia sinensis	110	450	150
Coscinodiscus excentricus	80	200	90
Ditylium brightwelli	90	410	90
Guinardia flaccida	400	—	30
Rhizosolenia stolterfothii	470	—	—
,, færœnse	—	780	—
,, sp.	—	80	—
Thalassiosira gravida	760	240	150
,, nordenskioldii	110	—	—
Thalassiothrix nitzschioides	360	620	—
Lauderia borealis	250	—	90
Chætoceros densus	40	—	30
,, decipiens	510	—	—
Ceratium fusus	10	—	—
Skeletonema costatum	580	—	150
Navicula sp.	—	—	30

After a further period of 15 days, having a daily average of 6·8 hours' sunshine, a series of observations were made on March 28th, when the maximum spring population was found. The composition of the flora had remained much the same except that Guinardia was present in some quantity at L_4.

Throughout this period of increasing diatom population between winter and spring, planktonic animals were not noticeably numerous, quite half the catch in the fine nets appeared to consist of diatoms.

Nevertheless, this maximum population only represents those diatoms which had not been eaten or died during the previous six weeks. Some 7000 units of plant pigment per cubic metre of water does not represent the six weeks' production of vegetable matter, for there is evidence that considerably more had been produced. I am indebted to Dr. L. H. N. Cooper for analyses showing the phosphate content of the water in the area. At L_4 the dissolved phosphate in the column of water from surface to bottom had fallen from 26 to $13\frac{1}{2}$ mg. P_2O_5 per $m.^3$ during this period of six weeks (Feb. 16th–March 28th), indicating that $12\frac{1}{2}$ mg. P_2O_5 had been utilised in the production of diatoms—on the assumption that the water-mass had not changed. Since the sea at the beginning of the period contained an equal quantity of phosphate farther out to sea, and at the end of March rather more than at L_4, and since the water in Plymouth Sound contains more phosphate than at L_4, the likelihood is that any movement of water to the L_4 position brought a little phosphate with it. Hence the value 12½ mg. utilised is if anything on the low side.

These values are expressed in the customary manner, no correction being made for salt error. If this be taken into account, the value 12½ becomes 15½ mg. P_2O_5 per $m.^3$.

I am indebted also to Dr. Cooper for analyses of the total phosphorus contained in a catch of diatoms. These consisted for the most part of *Biddulphia sinensis* and *Thalassiosira sp.* and were nearly free from zooplankton. A description of the method of analysis which was finally employed is published in this Journal, Vol. XIX, pp. 755–759. The pigment content of a part of the catch was estimated directly they were caught, and the remainder divided into three parts to allow analysis in triplicate.

The result showed that a quantity of diatoms containing 1000 units of plant pigment contained phosphorus amounting to 0·31 mg. when expressed as P_2O_5.

Several other catches, consisting mainly of diatoms, were analysed. They were not as free from animals and detritus as in this case, but after making allowance for this, they confirmed the value arrived at as representative for the mixed diatoms which flourish in winter. The assumption is made, pending further investigations, that the value is also more or less representative for summer diatoms.

From this it is deduced that at the time of the diatom outburst, when each cubic metre contained some 7000 units of plant pigment, the diatoms contained some 2 mg. P_2O_5. Since they had utilised over 15 mg. P_2O_5 during the previous six weeks, seven to eight times the quantity of diatoms found on March 28th had been produced. Seven-eights of this estimated six weeks' production had disappeared either by having been eaten, or much less likely by having died.

Neither this estimate, nor any one of those which follow, can by itself be considered as more than indicative. Each is subject to obvious reservations. But, taken as a whole, they present a consistent picture of a well, and often heavily, grazed pasturage of diatoms during the first half of the year.

The increase in population during the twenty-day period between March 8th and 28th at L_4 contained some 5000 units of plant pigment per cubic metre, and hence phosphorus amounting to 1½ mg. P_2O_5. The phosphate in the water utilised during this period amounted to some 7 or 8 mg. P_2O_5 per cubic metre after making allowance for salt error. This quantity of phosphate would be contained in diatoms having 22,000 to 26,000 units of plant pigments, or five times more diatoms than the observed increase in population. During this period of the spring outburst, conditions were clearly satisfactory for diatom growth, there was both sunshine and an ample supply of nutrient salts. It is improbable that diatoms died in any quantity ; however, if we imagine that all the phytoplankton present on March 8th died naturally before the 28th, a similar calculation indicates that four to five times the nett increase had actually been produced.

It appears, therefore, that throughout this period of rapid increase the diatoms were being well grazed by the herbivorous animals.

The rate at which the diatoms reproduced is of interest. During the 20 days the mean population or "breeding stock" contained some 4200 units of pigment. The total calculated production lies between 22,000 and 26,000 units of pigment. This points to the breeding stock having divided about six times, or, on the average, once every 3½ days. If the diatoms were not being grazed the actual increase in abundance could be accounted for by less than two divisions during the 20 days.

The First Outburst of Larvæ.

As already mentioned the catches consisted of diatoms with only a moderate or small proportion of animal plankton. On April 4th, one week after the observations of maximum diatom population, the catches were equally large or larger, but consisted mostly of larvæ with only a small amount of phytoplankton—most in the inshore water. The catches also contained a great number of small fæcal pellets, most of which were tinted green with plant pigment.

It is concluded that the outburst of planktonic larvæ which occurred during this week had grazed down the pasturage of diatoms. There is no reason to suppose that the diatoms had ceased proliferating, because there was still plenty of phosphate in the water (Fig. 5) and there was an average of seven hours of sunshine daily during the week. There is no evidence that the water mass occupying the area on March 28th had moved away by April 4th to be replaced by water from another area in which there had been different conditions for growth. Neither salinity nor phosphate content had altered materially. The character of the phytoplankton had changed, at the Cawsand position and at L_6 where the diatoms had remained most abundant some of the large *Biddulphia sinensis* and Guinardia remained, at L_4 these seemed to have been eaten, the more spiny Chætoceros and Rhizosolenia remaining, and the peridinians *Ceratium fusus* and *Peridinium depressum* appeared in the catches.

Unfortunately, only one haul was made below 20 metres on April 4th, from surface to near the bottom at E_1. The result showed water very barren of diatoms. This does not support the unlikely possibility that the diatoms had died in the surface layers and had sunk.

Throughout April and early May small diatom-feeding larvæ remained numerous and the phytoplankton sparse. At L_4 on April 26th the catch consisted for the most part of larvæ and numerous fæcal pellets, with *Chætoceros densus* and *Thalassiosira sp.* dominant amongst the few diatoms ; by May 11th *Rhizosolenia alata* had become dominant and the daily production of diatoms considerable.

Although the observations showed that the stock of diatoms at any time was small, the phosphate content of the water continued to fall. A decrease of about 8½ mg. P_2O_5 per m.^{3} between April 4th and May 11th at L_4 indicates the production of diatoms containing some 27,000 units of pigment in each cubic metre of water, or an average of some 700 units daily. The observations, which are admittedly insufficient, indicate that less than this quantity was present in the water on the average and suggest that the diatoms present had divided as often as twice daily to produce 27,000 units of pigment in 5 weeks.

The rate of production suggested by this calculation appears at first sight excessive. However, Gran (1933) found that Chætoceros at 1½ metres below the surface at Woods Hole, one month after midsummer, made seven divisions in three days and other species five to six divisions. In other words, they produced three times their own weight of vegetation daily. During this period at L_4, two months before the summer solstice, there was an average of 5·8 hours of sunshine daily. Certainly the water at L_4 was poor in nutrient salts compared with that used in Gran's experiments. From this it seems that although the calculated rate of production at L_4 may be excessive, it is not absurdly so.

To sum up, the evidence as a whole indicates that with lengthening days and increasing sunshine the stock of diatoms increased from February to March 28th, producing more daily than was eaten by the herbivores. Then a sudden outburst of larvæ rapidly ate down the stock of diatoms to a low level, and kept it eaten down closely for the following five weeks, during which time the small stock was producing vegetable food for the herbivores. Rough calculation, based on the assumption that water of different origin had not moved into the area, suggests that the stock was producing more than its own weight of vegetable food daily.

At Cawsand on May 11th the catch was composed as follows :—

Rhizosolenia alata . . .	3440 individual cells per litre.
,, *styliformis* . .	82
Ceratium fusus . . .	41
Guinardia flaccida . . .	20
Gyrosigma sp. . . .	40

comparable in cell contents to some 3900 cells of *R. alata* per litre, and contained 0·536 units of plant pigment per litre. Hence 1 unit of plant pigment was contained in about 7300 cells of *R. alata*.

THE OUTBURSTS OF *Rhizosolenia alata* IN MAY AND OF *R. stolterfothii* IN JUNE.

During the five days between May 11th and 16th the diatom population at both L_4 and the Cawsand station had doubled. At L_4 the diatoms consisted almost entirely of *R. alata*, which allowed another assessment of the unit of pigment to be made in terms of this diatom. A similar value was obtained, one unit of pigment being contained in 6950 individual cells. The species was a small form. At the Cawsand station the same species was dominant with some *Chætoceros densus* and Skeletonema.

On May 22nd an extensive series of hauls were made at L_4 and at positions 2 miles either side in a direction parallel to the coast, in order to investigate the uniformity of the population (p. 772). The diatoms again consisted almost entirely of *R. alata* which had attained a considerable density, over 30,000 cells per litre. The maximum occurred below the 20-metre level and doubtless exceeded 40,000 cells per litre in patches.

It is interesting to compare the density of this species in the Gulf of Maine, when a maximum of 50,000 cells per litre were found on August 4th, 1932, at 26 metres, less above and below, at one station—" a nearly maximal density " (Gran, 1933). The size of the cells may have been much larger, if they were one of the several other " forms " of this species.

By June 12th this population had been grazed down or had died down, much zooplankton and their fæcal pellets being present in the catch. The association of plants had changed to a very mixed plankton with *Ceratium fusus*, *R. alata*, and *styliformis* dominant. On both the 12th and 16th there was a greater density of population below the 20-metre level. On June 16th a haul was made several times up and down between the 20- and 40-metre levels (Fig. 3) which substantiated this vertical distribution, *R. stolterfothii* and *Guinardia flaccida* being dominant in the catch. By this time the upper 20 metres had probably been depleted of nutrient salts.

On June 20th an outburst of these two species was found close inshore, the hauls containing very little zooplankton.

On June 28th considerable quantities of these diatoms, mostly *R. stolterfothii* were found at L_4 below the 20-metre level. The dominance of this species persisted throughout July.

From the middle of June throughout the summer copepods were numerous.

During this period of dominance of *R. stolterfothii*, sporadic outbursts are indicated in the shallow inshore waters—the marked outburst on June 20th occurring at a time when zooplankton was for some reason scarce—and sporadic outbursts farther to seaward in the deeper water. The sections (Fig. 3) suggest that in June the zooplankton may have occurred in swarms, accounting for the uneven distribution of diatoms. Herdman (1922) notes that in the Irish Sea during the diatom outburst there is greater uniformity in adjacent hauls than at other times when a zooplankton was present. There is evidence of a lack of nutrient salts in the upper layers beyond the coast about this time (Fig. 5).

It was noted that zooplankton was relatively sparse, both when *R. alata* was dense in May and *R. stolterfothii* dense later, suggesting that the summer outbursts occur only when and where the demand of the herbivores slackens, and, naturally, where there are enough nutrient salts. I did not realise this early in the summer, and no measurements of the zooplankton were made, so the suggestion can only be put forward as such. The evidence so far accumulated points to the important part played by the herbivorous zooplankton in regulating the vegetable population. If this is not the explanation of why some species of the mixed diatom population in March did not proliferate and use up the remaining nutrient salts, we have to fall back upon some idiosyncrasy of the diatoms themselves, or lack of some unknown constituent in the water which is but slowly reformed, as explanation. Of these we have no real evidence ; certainly cultures of oceanic diatoms tend to die out, but then such cultures are immensely dense compared with conditions in the sea. The suggested explanation can account for smaller outbursts occurring at intervals or sporadically during the early summer while there are still nutrient salts in the water. When it is borne in mind that diatoms can, and do, more than double their weight daily in the sea under optimal conditions, an explanation is necessary to account for some of the numerous species present not increasing in numbers sufficiently to use up the available nutrient salts before the end of the spring.

THE AUGUST SCARCITY.

By August 1st diatoms, of which *R. stolterfothii* remained dominant, had become scarce. On the 15th and 29th they must have been very scarce indeed. Many pigmented copepods were present, which rendered colour comparison of the extracted pigment uncertain, so that all one could do was to obtain a maximum value for the yellow-green plant pigments in the acetone extract. It is probable that these maximum values, small though they are, are themselves considerably greater than the actual. During this period lack of nutrient salts limited the production ; on the 9th the surface water was found free from phosphate and at 49 metres only 2 mg. P_2O_5 per m.^{3}. Since mid-July life had become dependent upon the phosphate and ammonium salts being excreted and reformed from dead organisms.

It is of interest to consider the rate at which nutrient salts are supplied to the water during the summer, although these observations only allow the roughest calculation to be made. If we assume that throughout August phytoplankton in the L_4 water contained no more than 50 units of pigment per m.^{3} and the organisms reproduced daily—the month's production contained 1500 units of colour or 0·47 mg. P_2O_5 per m.^{3}. This suggests that until the end of August and the dying down of the summer zooplankton, only a very small quantity of phosphate was regenerated and used again, and that the phosphorus abstracted from the water in the form of phosphate by the phytoplankton earlier in the year was kept almost entirely locked away as phosphoproteins in the animals until the end of August in this relatively shallow area. However, farther to seaward we have evidence that regeneration of phosphate took place in considerable quantity before the end of July in several previous years (Atkins, 1930).

In the shallow inshore waters, which had probably some nutrient salts available, diatoms were present during August when the water offshore was barren.

The Autumn and Winter Conditions.

In September the copepods in the catches decreased and a mixed diatom plankton appeared, *Rhizosolenia styliformis* and *Biddulphia sinensis* being dominant. On the 19th, at both surface and bottom, the water contained 19 mg. P_2O_5 per cubic metre, indicating that death and decay of much of the summer plankton had taken place. There seems to be a possible lag in time between the proliferation of the diatoms and the appearance of a supply of phosphate. This was expected, because in previous years, when analyses of nitrate in the water were made, the regeneration of nitrate was found to have taken place a little later than that of phosphate. No measurements of the quantity of zooplankton in the water were made and no evidence obtained of the date at which great quantities apparently died, nor have we any knowledge of the length of time taken for phosphate to be regenerated from dead zooplankton, a question open to experimental attack. It is thought that rather wholesale death of herbivorous organisms and some of the carnivores dependent upon them for food was brought about at the end of August through starvation.

By the end of September zooplankton was sparse. During October and November there was much sunshine and few herbivorous animals in the catches; the diatoms increased, maximum catches being obtained on November 22nd when the same two diatom species were dominant as in September.

With regard to the autumn outburst Herdman remarks that this only takes place when the weather conditions are satisfactory. With respect to illumination, the autumn of 1933 had considerably more sunshine than normal in September and slightly more than normal in October and November.

The observations made during these two months show an even vertical distribution at L_4, which does not suggest a loss due to diatoms dying and sinking to the bottom, which undoubtedly takes place at some times and in some areas. In fact, no evidence of this has emerged, although it may sometimes occur in this area.

During the winter months of December, January, and February, 1934, considerable quantities of diatoms were present. At no time was the water other than well-seeded with diatoms. The community was very mixed, Biddulphia, Coscinodiscus, and Thallassiosira species being dominant. In one respect these winter months were quite unusual, considerably less phosphate being found in the water than in previous years. In view of this unusual condition it is not possible to judge whether the rather considerable diatom population during the winter was a normal phenomenon.

The Inshore Station.

The quantity of phytoplankton at the inshore station off Cawsand remained low throughout the year (Fig. 5). Except during April and August there was consistently less than farther out to sea. During the winter months this may be due to the lesser transparency of the water ; but no reason is obvious for the small quantities found in summer, because in previous years the water here was found to be richer in nutrient salts than farther to seaward.

DISCUSSION.

The first half of the year 1933 was marked by much sunshine, an absence of strong winds, and a rather early spring maximum of diatoms. The seasonal change in dissolved phosphate in the water as it was utilised by the phytoplankton was in no way remarkable. A proliferation and spring maximum of diatoms, their very sudden decrease in numbers *before* all the dissolved phosphate is used up, and secondary maxima in the early summer are quite usual.

The data collected allow a picture to be drawn which accounts for the big changes which occur in the phytoplankton population during the year. The estimates arrived at, upon which this picture of the regime of the vegetation depends, are based to some extent on certain assumptions which are not rigidly true. However, even if some of the true average values are grossly different from those estimated, the same general picture is still presented, only modified in degree. Changes of several hundred per cent are being dealt with, so that errors amounting to 50 or even 100 per cent due to sampling or renewal of the water from elsewhere do not necessarily destroy the general picture.

In the first place it is concluded that several times more vegetation is produced during the few weeks' proliferation than is found at the spring maximum. The decrease in phosphate content of the water during this period was in no way unusual. Atkins records the daily decrease in phosphate at E_1 during spring diatom outbursts as varying between 0·40 and 1·06 mg. P_2O_5 per cubic metre for the whole column of water from surface to bottom. During the few weeks of the spring increase in Loch Strivan, between March 23rd and April 20th, 1926, Marshall and Orr record a fall from 44 to 30 mg. P_2O_5 per m.^{3} in the column of water from surface to bottom, that is a fall of some 20 mg. P_2O_5 per m.^{3} after allowing for salt error. The spring maximum of diatoms at L_4 as found on March 28th may have been less than the average maximum attained, although there is no evidence to suggest this. If we imagine that the true average was even three times the quantity found, it then contained phosphorus amounting to about 6 mg. P_2O_5 per m.^{3}, which is less than half the decrease in dissolved phosphate during the previous six weeks.

It is next concluded that this excess of production over increase in population was eaten and did not die. There was no evidence of dead diatoms in the catches, and an enormous death rate amongst *actively dividing* diatoms is against our present knowledge.

It is then concluded that at the end of March the population was rather suddenly eaten down to a low level. For this to happen would only require a moderate increase in the intensity of grazing by the herbivores, if their activities in eating the greater part of the production prior to the end of March is admitted. We have the general observation of a great increase in the quantity of zooplankton on April 4th, and the very noticeable presence in the catch of great quantities of fæcal pellets tinted green with diatom remains, which by itself is strong circumstantial evidence. If this is not the explanation of the decrease in diatom population, we have not only to fall back upon their death during a time when there was ample illumination and ample nutrient salts in the water, due to some peculiar idiosyncrasy of the plants themselves, but to neglect the evidence of fæcal pellets, of increased zooplankton, and lack of dead diatoms on April 4th.

During the early summer the greater part of the catches consisted of zooplankton, requiring a considerable daily ration of diatoms for their maintenance. If we concede that during March, when the relative proportion of herbivores was much less, a considerable part of the daily production of diatoms was eaten, it follows that during the early summer grazing was very intense. Fluctuations in the numbers of herbivores can readily account for the secondary diatom maxima during early summer.

Such fluctuations amongst copepods, which perhaps make up the greater number of herbivores, are known to occur, cf. *Calanus finmarchicus* (Nicholls, 1933). This provides a simple explanation of a hitherto unexplained occurrence.

During the winter months at the beginning of the year, the amount of sunshine and transparency of the water without doubt keeps the daily production of diatoms from greatly exceeding the herbivores' requirements, in March the lengthening days and greater illumination allow an increase in vegetation. From then onwards the diatom population is regulated by the intensity of grazing, until it has used up the nutrient salts in the water. The utilisation of the nutrient salts and onset of barren conditions would presumably occur in the spring, if the herbivores did not keep the breeding stock of plants eaten down.

It is seen that the available plant food for marine animals varies greatly throughout the year. There is good reason to suppose that the periods of plenty and periods of famine do not occur at the same time in different years. The incidence of sunshine varies greatly, some weeks being bright and allowing considerable growth of the phytoplankton, other weeks dull and so limiting it, particularly between October and April. The density of herbivorous animals—mostly the smaller zooplankton—doubtless varies at any particular time from year to year, on account of there being sufficiency or insufficiency of plant food, of the balance between herbivores and carnivores, and of temperature affecting their breeding time. Shortage of vegetation occurred in April at L_4 during sunny weather when there was plenty of nutrient salts in the water.

An intimate relation or balance exists between the ever-varying populations of carnivores, herbivores, and vegetable food, which in its turn is sometimes controlled and always affected by the available nutrient salts and illumination. If the proportion of carnivorous to herbivorous animals is displaced for a period by an "abnormally" large number of carnivores, then the diatoms are free to flourish and increase their population. If, on the other hand, the balance is displaced for a period by an "abnormally" small proportion of carnivores, then the herbivores freed from their enemies can flourish, keep the breeding stock of vegetation closely grazed, and by so doing limit their own increase. This would automatically delay the utilisation of nutrient salts.

The total productivity of the sea in most northern areas is limited by the nutrient salts available in the illuminated upper layers, for these are entirely or almost entirely utilised before the end of summer. However, in the Southern ocean only a part is utilised before the end of summer. This unexplained occurrence leaves a gap in our present knowledge of the productivity of the sea. In addition to slower rates of proliferation in colder waters, to the diatoms being subject to vertical movements which may carry them rather soon below the range of sufficient light, the herbivorous population grazing upon them will tend to delay the utilisation of the very rich supply of nutrient salts, as it does elsewhere.

SUMMARY.

Vertical hauls were made with a very fine silk net having a meter attached, which measured the volume of water filtered, at positions off Plymouth throughout the year 1933.

The quantity of phytoplankton was assessed from its content of yellow-green colouring matter, and expressed in terms of " units of plant pigments " per cubic metre of water filtered.

The diatom population per cubic metre at Station L_4 on March 28th was estimated to contain phosphorus amounting to 2 mg. P_2O_5, whereas dissolved phosphate amounting to some 15 mg. P_2O_5 had been used from each cubic metre of water by the diatoms during the previous six weeks.

It is concluded that the production of phytoplankton during this period greatly exceeded the quantity found at the height of the spring outburst, and that the excess had been eaten by the herbivorous zooplankton.

Between March 28th and April 4th the phytoplankton decreased to one thirty-fifth, coincident with a noticeable increase in zooplankton. Great numbers of fæcal pellets tinted green and largely composed of the remains of diatoms were found in the catch on April 4th.

It is concluded that the sudden decrease in vegetation after the spring maximum was due to increased intensity of grazing by the increased numbers of herbivorous zooplankton.

Evidence is presented that between April and the end of July the phytoplankton population was regulated by the intensity of grazing by the zooplankton. Two secondary diatom maxima occurred during this period. A rough calculation indicates that the phytoplankton was producing more than its own weight of vegetable matter daily during the first five weeks of this period, the zooplankton meanwhile eating this daily supply of vegetation.

During August the water was almost barren of vegetation, except at the inshore station, coincident with almost complete lack of dissolved phosphate in the water at a short distance offshore.

A well-marked autumn outburst of diatoms occurred in October and November, and during the winter months the phytoplankton was over eight times more than in August.

I take this opportunity of acknowledging the help and co-operation of Dr. L. H. N. Cooper who has carried out all the phosphate analyses and, after developing a suitable method, the analyses of organic

phosphorus, of Dr. M. V. Lebour for identifying many diatoms, of my colleagues, particularly Mr. F. S. Russell, for much information and helpful suggestions, of the personnel of the S.S. *Salpa* and M.B. *Gammarus* for patiently hauling the net through several miles of sea.

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On the Biology of *Calanus finmarchicus.* V. Seasonal Distribution, Size, Weight and Chemical Composition in Loch Striven in 1933, and their Relation to the Phytoplankton.

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With 9 Figures in the Text and Plates I and II.

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INTRODUCTION.

THE work on Calanus carried out in 1932 (Nicholls, 1933, Part I) in the Clyde Sea-Area showed that the course of events was very much the same at all four stations worked. It was felt, however, that more frequent observations would be useful for understanding the fluctuations in the population and for relating them to the food available as microplankton. Loch Striven was therefore chosen, primarily for the convenience of its position, and was visited weekly. Previous work (Marshall and Orr, 1927) has shown that this loch, although not so isolated as Loch Fyne, is little affected by ingoing or outgoing currents, and the population can be taken as self-contained. The position chosen, Station VIII (see Part I, Text-figure 1), was situated in mid-loch and had a maximum depth of about 70 metres.

Since it was known that the autumn–winter stock of Calanus starts moulting early in the year, the first visit was made in the middle of January. Weekly visits were then continued until the end of August, by which time the population had returned to its normal autumn–winter state (mainly Stage V). Two further visits in September and October confirmed this.

A series of five vertical hauls was taken each time with the Standard Net described in Part I. Five hauls were taken because of Gardiner's statement (1931) that of a large number of comparable hauls only about one in five is likely to deviate considerably from the average. Any haul which was by inspection a freak, being either much richer or much poorer than the others, was therefore rejected. On three occasions all five hauls were counted separately; on two of these there was a gradual diminution of numbers from first to last. Although the taking of a number of hauls in this way probably diminished considerably the errors inherent in the method, yet it does not do away with them entirely. The five hauls were taken within such a small area that they are not necessarily representative of the loch as a whole.

From March 27th onwards one haul in every five was taken in two sections (from the bottom to 10 metres and from there to the surface), in order to throw further light on the seasonal changes in vertical distribution. This divided haul was always counted, but when it disagreed noticeably from the average of the other four, in numbers or composition, it was ignored in estimating the average number per haul.

Samples of all the copepodite stages were taken from the standard hauls for measurement. On a few occasions in spring, when adults were scarce, additional vertical hauls were made with a one-metre stramin net to provide sufficient material for measurement. Methods of preservation, sampling, counting, and measurement were the same as described in Part I and Part II (Marshall, 1933).

Further hauls were made with the stramin net to provide material for weight determinations and chemical analyses, and these catches, suitably diluted, were taken home alive in large jars of sea-water. These hauls were usually taken horizontally in deep water, so that the Calanus caught were not necessarily a fair sample of the population. Measurements show that the majority of the Stage V and adult Calanus are caught, but that when they are small a few of the smallest may be lost by passing through the meshes of the net.

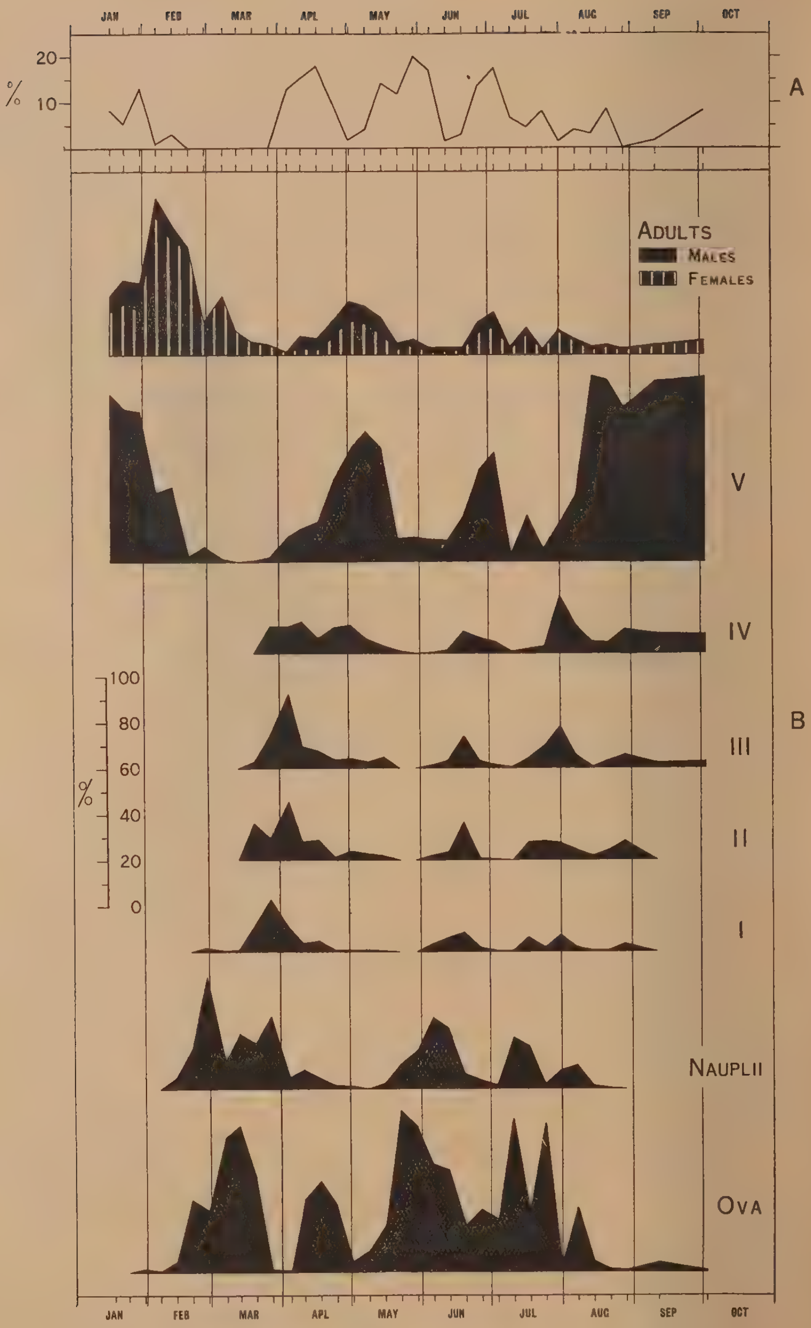
Water samples were taken with the insulating water-bottle at the surface and 30 metres, and the temperature noted. Samples from each were subsequently centrifuged and the number of organisms counted. Although counts made at only two depths do not give a detailed idea of the course of events in the microplankton, yet they are usually sufficient to show whether a diatom increase is present or not.

SEASONAL DISTRIBUTION.

The course of events this year was similar to that found in 1932. The autumn-winter Stage V Calanus moulted into adults through January and February and gave rise to the first brood of eggs. This is clearly seen in Plate I (percentage composition) and Tables I and II, but owing to the low numbers at that time the presence of this breeding period cannot be detected in the diagram showing numbers per haul. The first increase in numbers is seen at the end of March and beginning of April when the Calanus from the first brood of eggs were coming to maturity. One point must be mentioned about the catches from April 17th to May 1st. The number of copepodites present was much too large when we consider the number of eggs found in the previous weeks. The number of copepodites must always be *apparently* larger than the number of eggs which produced them because the copepodites stay longer in each stage than do the eggs, which remain as such only for about 24 hours, but this is not enough to account for the discrepancy. It must be noted, however, that at this time diatoms were very abundant. These would clog the meshes of the net and so reduce the amount of water filtered, particularly in the upper layers where the eggs and nauplii live (p. 814). Further, in the early part of March, from the number of females present one would have expected the number of eggs to be higher.

It will be noticed that the Calanus of the first brood of eggs were accumulating as Stage V in April and May. Only a few of these went straight through to adults and these produced a small brood of eggs during April. These eggs, however, were not followed by any considerable number of nauplii and young stages ; that is, the brood for the most part failed to develop. Only a few of the earliest eggs were found as nauplii. The failure of this brood is clearly seen in Text-figure 1. The Calanus which had accumulated as Stage V during this period moulted into adults about May 22nd and these produced the true second brood of eggs which lasted until about June 19th. This brood went through successfully to adults and these in turn produced another brood, the third, in July. Of the copepodites resulting from this brood many did not go through to the adult state but remained to form the autumn-winter stock of Stage V which was clearly established by August 14th. The few which did moult produced the small subsidiary broods of eggs in August and September, the survivors of which went to swell the stock of Stage V. One other point must be mentioned : the curious fall in numbers on July 17th. This fall is almost entirely in egg numbers since the actual numbers of nauplii and copepodites follow the usual course.

Natural mortality accounts for the fall in numbers after each breeding period and is most marked in the eggs and nauplii.



TEXT-FIG. 1.—A, The percentage of females bearing spermatophores. B, The succession of developmental stages through each breeding period.

FERTILIZATION AND BREEDING.

From April onwards the female Calanus measured alive for weight determination were examined also for the condition of the ovary. They were divided into four groups (Table V): (i) early state, in which the eggs in the ovary were small and there was only one row of small eggs in the oviduct; (ii) medium state, in which the eggs in the ovary were enlarging and there were several rows of small eggs in the oviduct; (iii) mature state, in which the oviducts were full of large eggs; and (iv) spent state, in which the ovary was degenerating or had disappeared. It was not always easy to distinguish between the four types and a certain amount of overlapping must be allowed for. Rough observations from January to March, before the first breeding period, showed that on February 20th there was a large proportion of the females in the early state. On March 7th the majority were mature and on March 27th a large number was spent. This agrees well with the production of the first brood of eggs. In the same way from April 4th to May 15th there was a large proportion of early and medium state females, those which were about to produce the abortive and the true second brood, and a large proportion again on July 3rd before the third brood. After this mature females always predominated. In September the number of females decreased but the majority still remained in the mature condition. The small number of spent Calanus probably indicates that females die soon after reproduction.

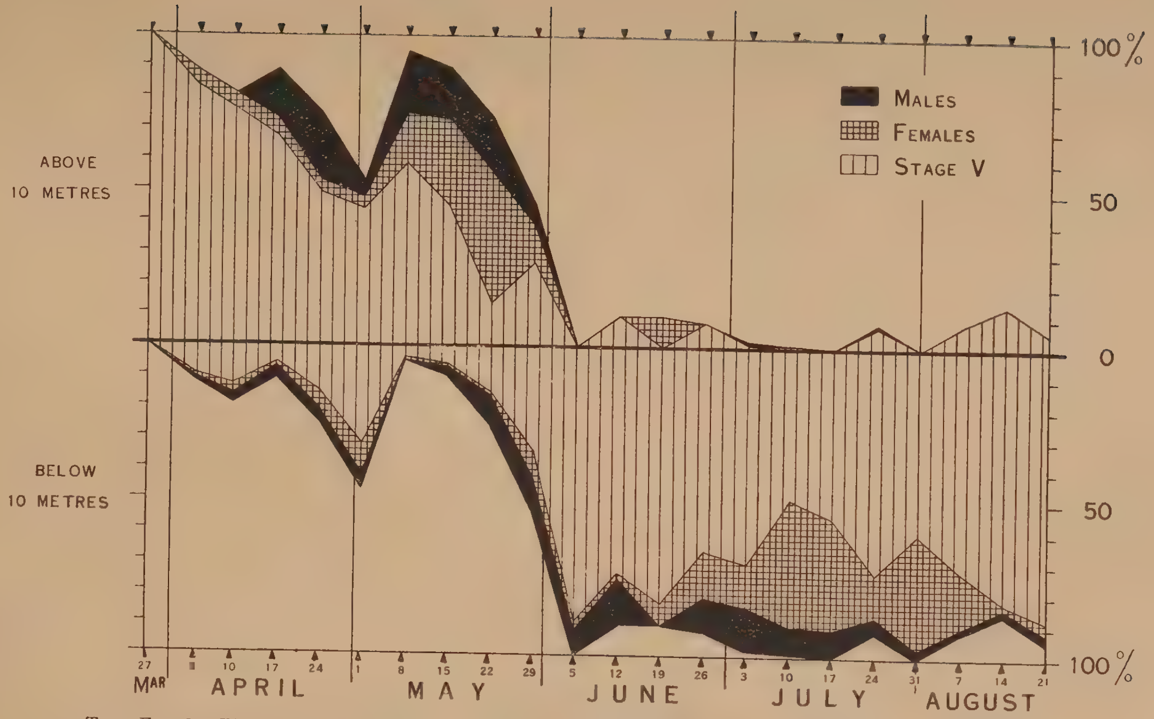
The percentage of females (in the standard hauls) bearing spermatophores rises before each brood of eggs (Table V and Text-figure 1) and is usually greatest when the proportion of males is at its maximum. Thus there is a peak in spermatophore-bearing females on January 30th before the first brood, on April 4th to 17th before the abortive beginning to the second brood, on May 15th to June 5th before and during the true second brood, and from June 26th to July 3rd before the third brood. After this the proportion was never high and the small peaks do not agree with the subsidiary broods. In this area the majority of females carry one spermatophore only, although occasionally two or three or even more are found. The males were never as numerous as the females except in April, but the disproportion is not so great as that described, for instance, in the North Sea (Gibbons, 1933). It is interesting to note that on several occasions Stage V Calanus were found with several spermatophores attached and in one case the number was as high as 13. These were usually distributed indiscriminately over the urosome and caudal furcæ but one or two were found attached to the posterior region of the thorax and fifth pair of swimming feet.

When the state of the ovary in spermatophore-bearing females is examined, it is found that spermatophores are much more frequent in the early stages than in the later. If we take early and medium state females together we find that of the 674 examined 17·4% carried spermatophores, while of the 1473 mature females less than 1% did so. One spent Calanus out of the total number of 38 had a spermatophore attached. These figures indicate clearly that the spermatophore is normally lost at a fairly early stage of development of the ovary. In recently moulted unfertilized Calanus the sacs opening on the genital segment are colourless and apparently empty, but in the great majority of the females found in the plankton they are dark in colour and appear to be full, presumably with the contents of the spermatophores. The spermatophores attached to the females are often empty. It is suggested that the sperm are stored in these sacs until spawning takes place and that some are passed out along with the eggs, but this needs confirmation by experiment. It may, however, be noted in support of this suggestion that in several other copepods the spermatozoa reach the eggs only when these are being spawned (Matscheck, 1909 ; Gray, 1929).

Immediately before the eggs are spawned they swell up and become granular in appearance. They are then squeezed out through the genital aperture as a string of sausage-shaped masses which separate and round off in a few seconds. Numerous females have been thus observed laying eggs on a slide and in several cases the numbers have been counted. The greatest number counted was 70. This agrees with the number suggested in Part I, but it is possibly exceeded at times.

VERTICAL DISTRIBUTION.

It has been shown before (Nicholls, 1933, Part III) that during the day in this area adult and Stage V Calanus normally live in deep water, but that at certain times of the year they may be found near the surface. Text-figure 2 illustrates their vertical distribution during the period from March 27th to August 21st, during which time one haul was divided at 10 metres. Numbers (Table II) above 10 metres were multiplied by six in order to make possible a fair comparison of the density above and below this level, since there was about six times as much water below as above. Young stages were not taken into consideration since their normal distribution is above 30 metres (Part III). It will be seen that from March 27th till May 29th Calanus in Loch Striven were inhabiting the upper 10 metres continuously and almost exclusively. After that date on no occasion were they found above 10 metres to any extent. It is interesting to note that the period in which they were moving down coincided with the transition period between the first and second broods, at which time Stage V and adults from the first brood were dying out



Text-Fig. 2.—The vertical distribution of Calanus in the divided haul during the three main breeding periods. (Based on Table II).

and those from the second brood were appearing in the catches. This indicates clearly that it was the first brood alone which showed this unusual vertical distribution. Gardiner's (1933) results on diurnal migration in the North Sea also showed Calanus more abundant near the surface than below in May. A comparison with last year's results when the hauls were divided at 30 metres shows that this phenomenon is not of regular occurrence. On two occasions in 1932 Calanus were noticeably more abundant above 30 metres than below and these were not restricted to the first brood.

SIZE, WEIGHT AND TEMPERATURE.

Where possible, samples of at least one hundred of each of the six copepodite stages of Calanus taken from the standard hauls were measured. The size-frequency distribution throughout the year is shown in Plate II, and the median lengths of the cephalothorax in Table III and Text-figure 3. The small size of Stages II and III partly accounts for the high values on the size-frequency curves for these two stages. All except Stage I copepodites were measured on the same scale; Stage I were so small that they were measured under a higher magnification. This naturally makes the areas covered by their frequency distribution curves smaller than those of other stages, but the lengths of the base lines are still strictly comparable.

From January to the middle of March only Stage V and adults were present; for most of this time only females were present in numbers sufficient to measure. The sizes fluctuate considerably, but this is partly because the numbers measured were very small.

On March 20th the first of the new brood appeared as Stage I and II copepodites; by March 27th they had developed to Stages III and IV, and by April 4th to Stage V and adults. From April 4th the size of each of these stages increased and the largest Calanus were found on April 24th. The female Calanus found on this date measured 2·82 mm. as compared with 2·41 mm. on March 27th. The females during this time were a mixture of autumn–winter stock and first brood Calanus, and the dying out of the former can be seen in the frequency distribution curves (Plate II). The curves are bimodal and the lower mode corresponding to the small autumn–winter stock gradually disappears. After April 24th

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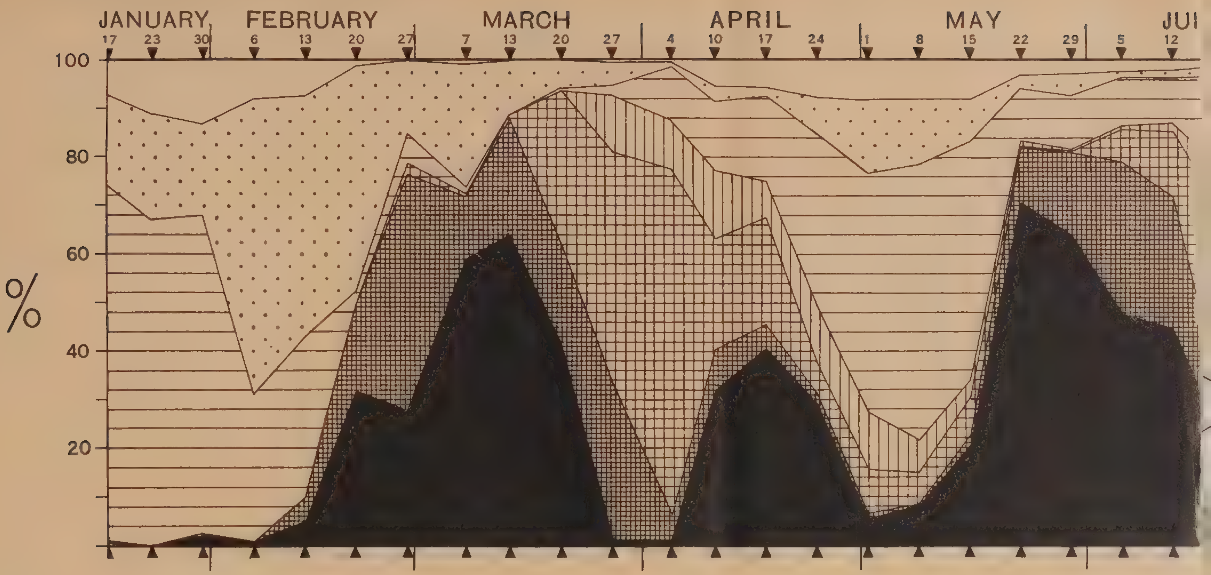
PLATES.

PLATE I.—Chart showing numbers per haul and percentage composition of population of *Calanus finmarchicus* during 1933.

PLATE II.—Curves showing the percentage size distribution of Calanus in Loch Striven, 1933. Left-hand side: thick line, males; thin lines, Stages V, III and I. Right-hand side: thick line, females; thin lines, Stages IV and II.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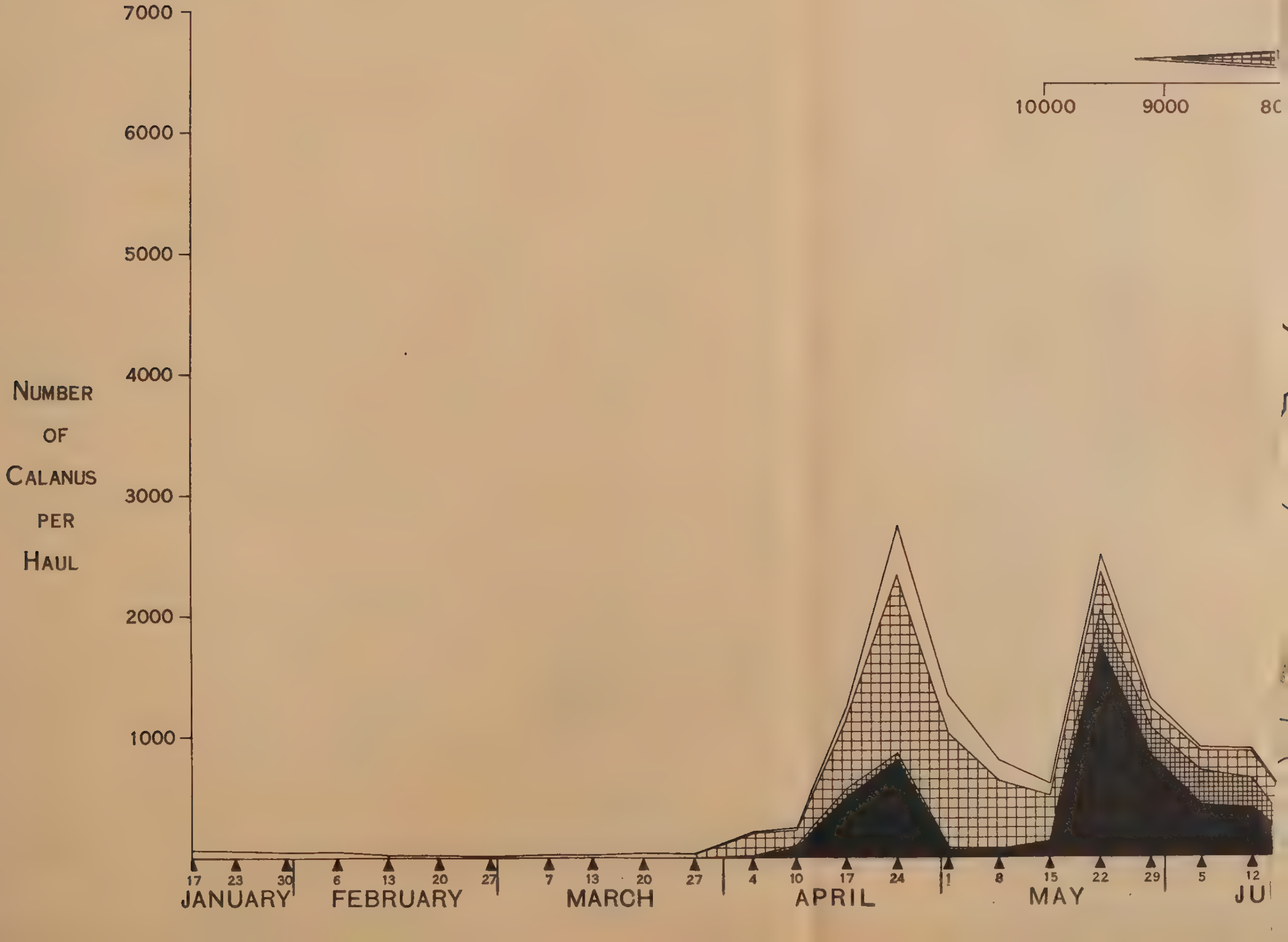
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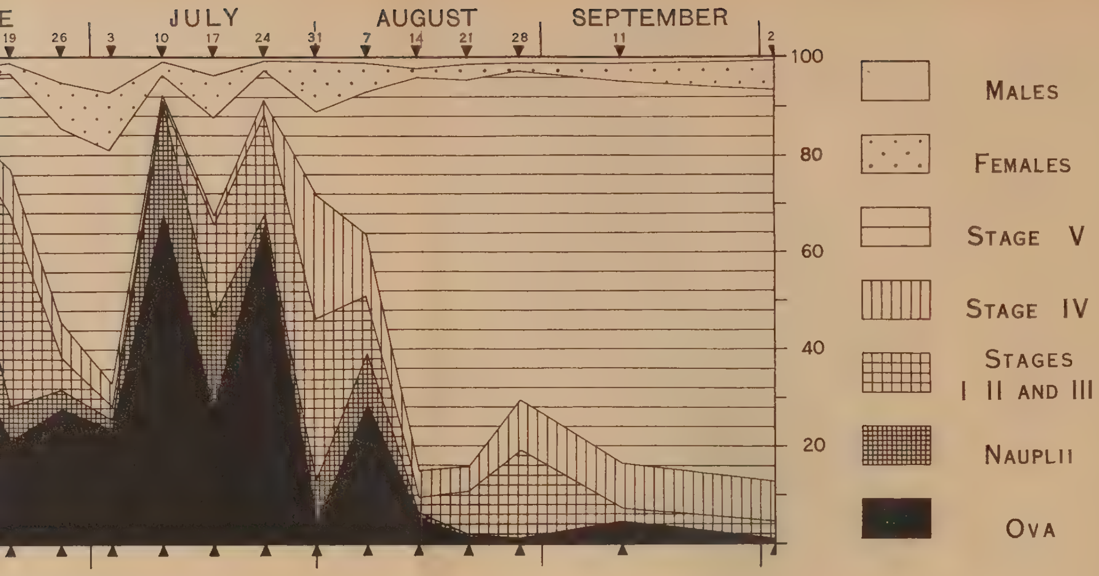
PLATE I.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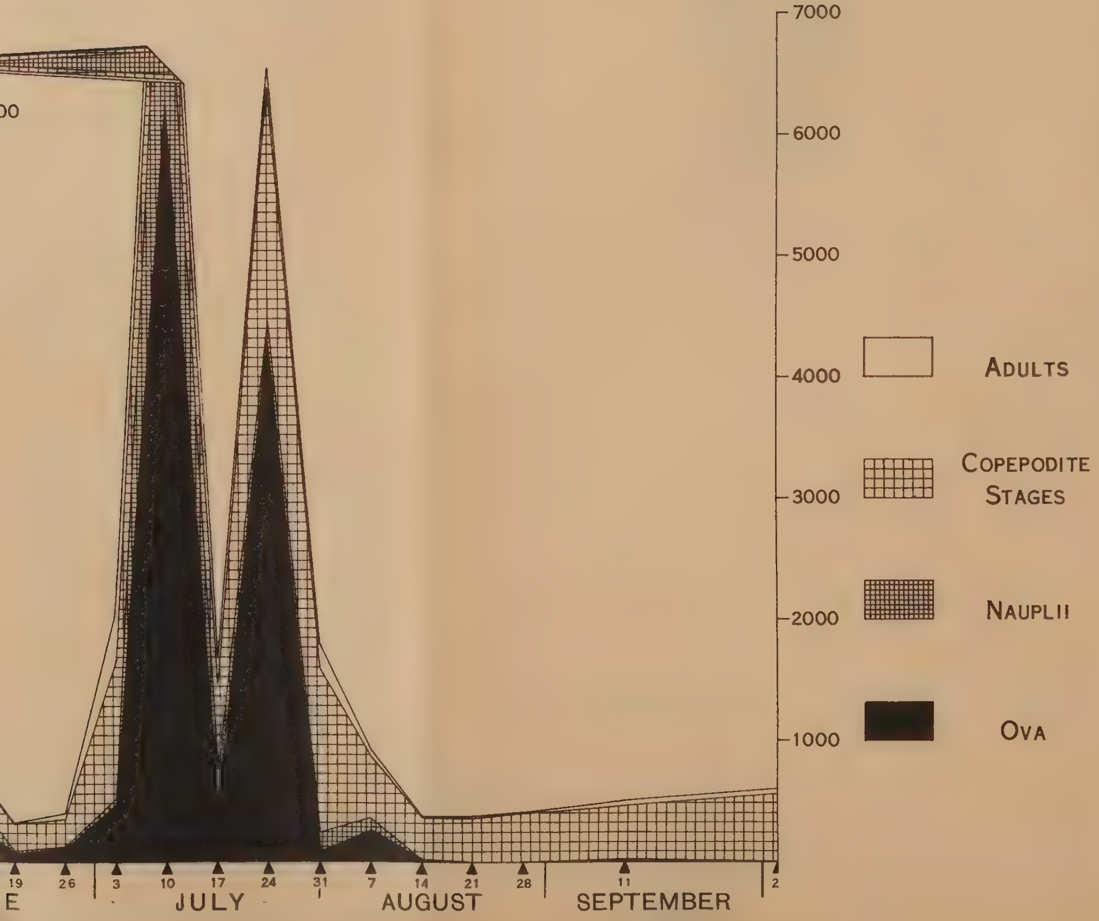
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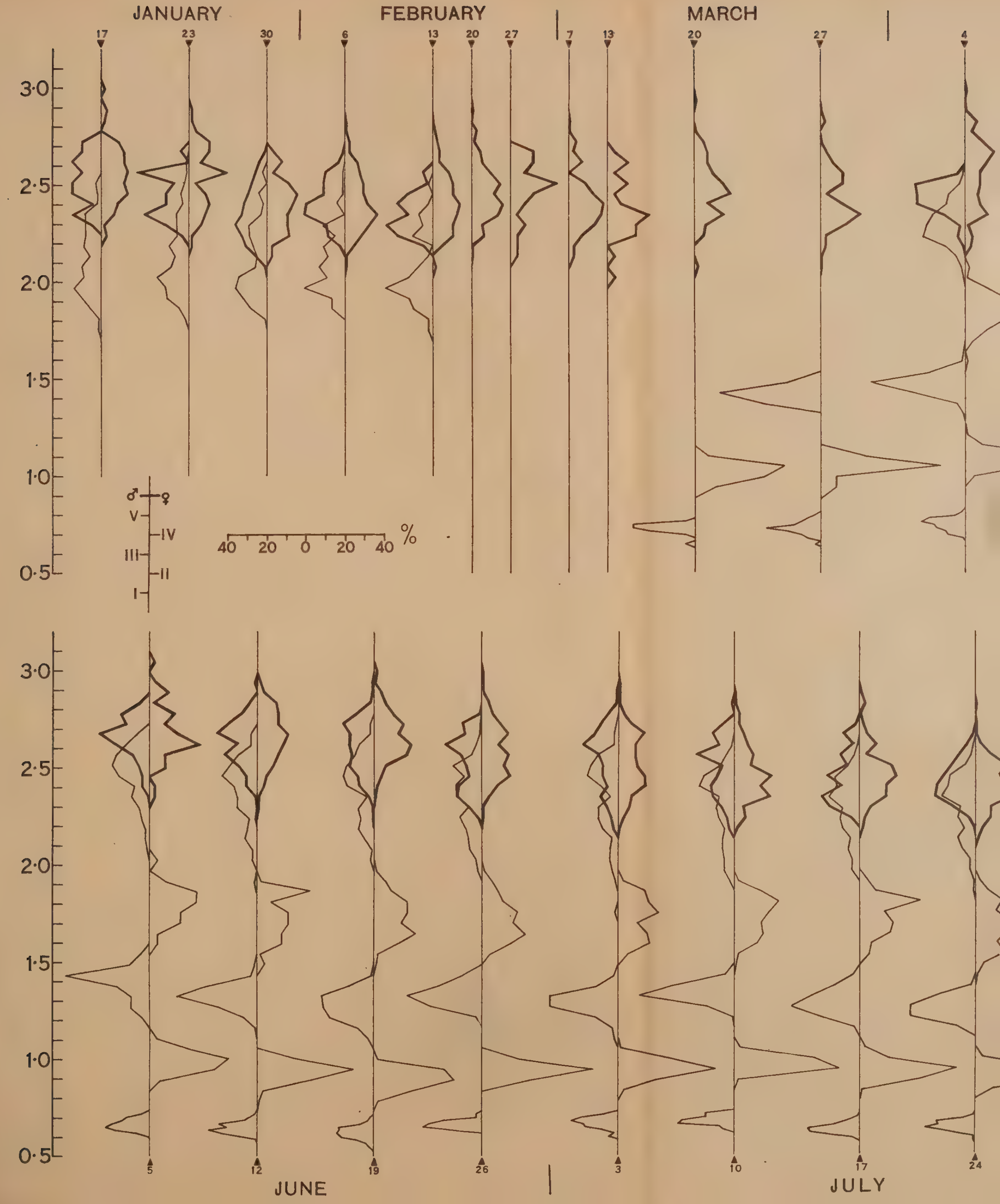
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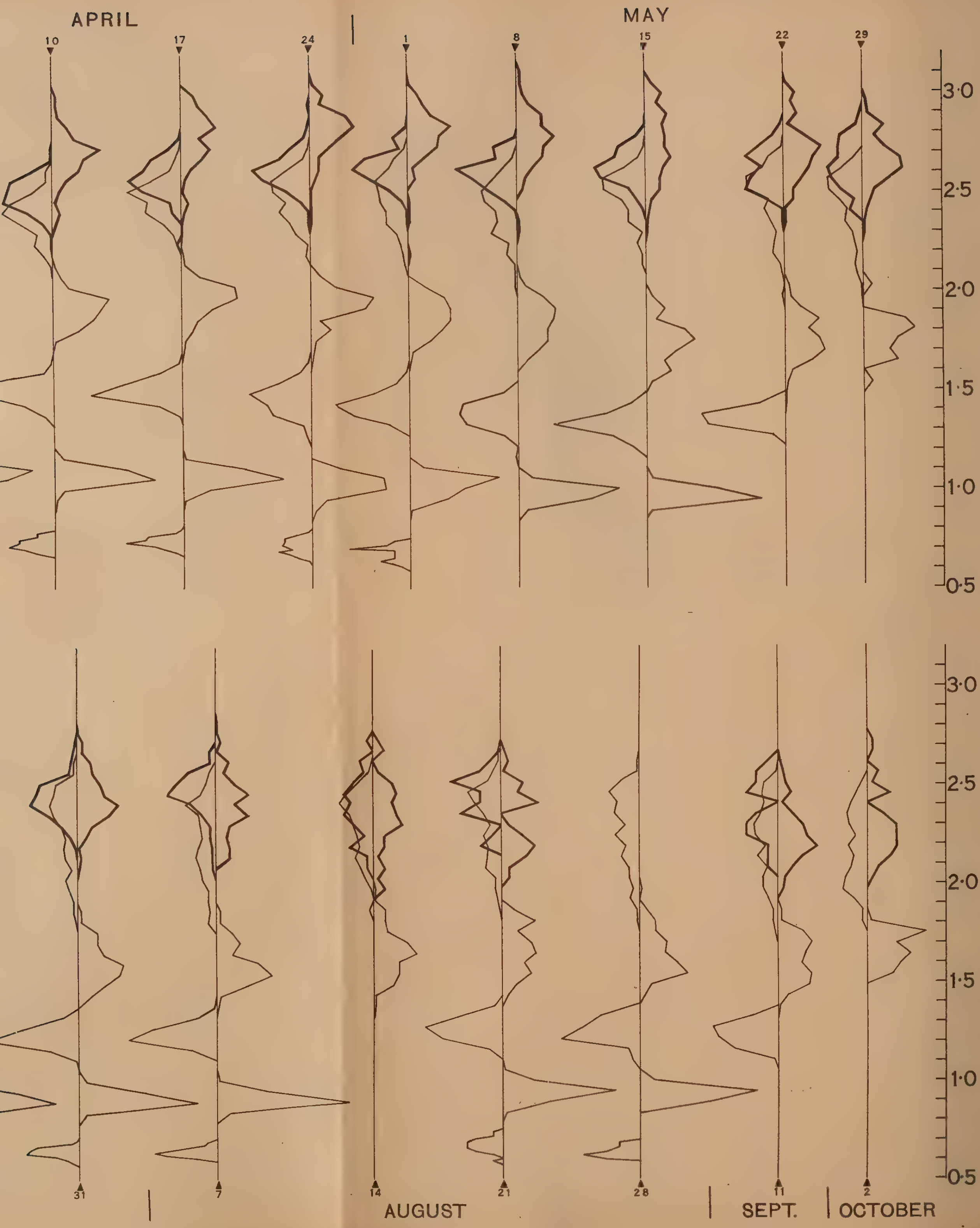
PLATE II.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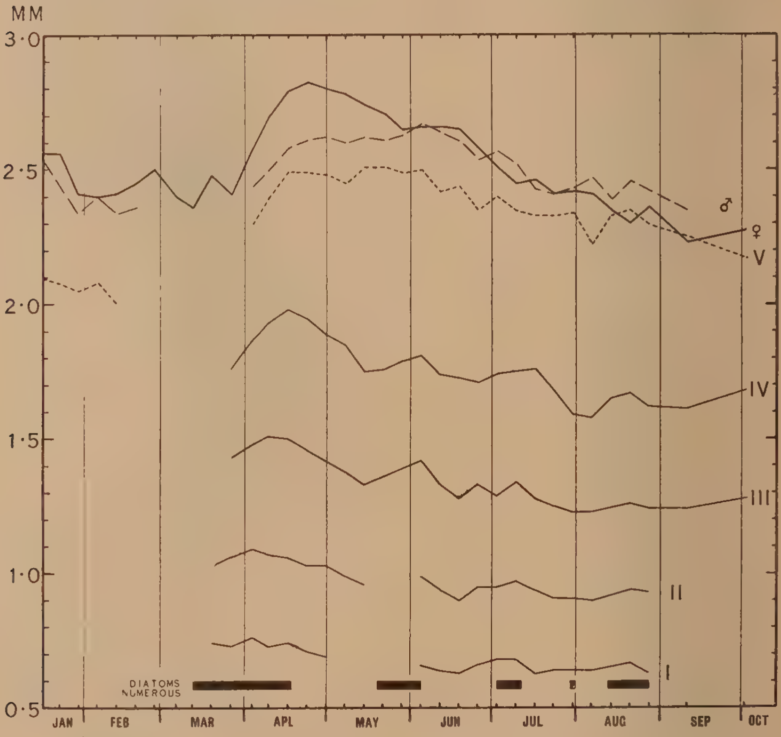
the size of all stages except Stage V and males fell until May 22nd or 29th, when the fall was checked, and in the younger stages the size actually increased a little. This corresponds to the appearance of the second brood. There were not enough of Stages I and II to measure. Males remained fairly constant in size and rose to their maximum for the year (2·67 mm.) on June 5th at the time of the second brood. The Stage V Calanus did not show the gradual fall in size either, but this is probably because in May they were accumulating instead of moulting to adults and the large ones remained to increase the average size of the stock. After the second brood, up to the middle of July, there was again a fall in size in all stages, but this was not regular and showed minor increases. The third brood appeared as Stages I, II, and III on July 10th, as Stage IV on July 17th, and as Stage V and adults, though less clearly, on July 31st. There was an indication of a subsidiary fourth brood towards the end of August. Since only a small proportion of these two broods became adults, a marked increase in adult size is not to be expected. In August and September the sizes of adults and Stage V approached each other, and in some cases the Stage V were actually larger than the females.

It seems certain, then, that while there was a gradual fall in size throughout the summer, this fall was temporarily checked at the time of the production of each new brood. In 1932 (Part II) it appeared that the Calanus from eggs spawned at the beginning of the breeding period were larger than those developing from eggs spawned at the end. This may be true in some cases this year, but it was certainly not so for the first brood in which the young stages (II–V) show that the size first increased and then decreased.

The fluctuations in dry weight of Stage V and adult Calanus are shown in Table V and Text-figure 4A. These weight determinations were made as described in Part IV (Orr, 1934) and usually on 100 individuals. The weight of Calanus naturally depends to some extent on its size, but the relation is not as close as might be expected (see below). Those which were weighed were also measured and the change in size in these samples agreed closely with the weight curves. A comparison of Text-figures 3 and 4B shows that they agreed also with the size samples from the standard hauls, especially the adults.

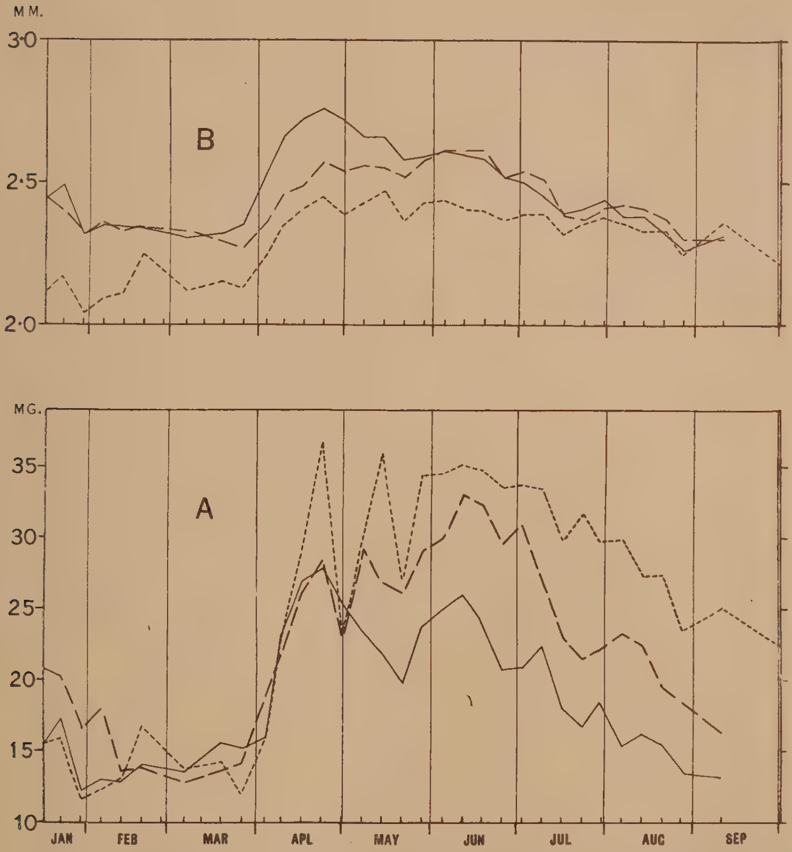
The samples were taken with a stramin and not with a fine silk net, so that one might expect them to be on the whole larger; on the other hand, these Calanus were measured alive and formalin fixation increases the size a little. Allowing for this increase after fixation the size of the adults in the two sets of measurements agrees very well. The main divergences occur in Stage V, but are, however, much larger than can be accounted for in this way, and must be caused by imperfect sampling. Stage V predominated in the catches from April onwards, and though it was often necessary to go through the whole catch to obtain sufficient adults, the required number of Stage V was obtained from one jar which represented only a small fraction of the catch.

From January to March Stage V and adults weighed very nearly the same in spite of Stage V being considerably smaller. At this time the numbers of males and Stage V available for weight determination were occasionally very small (Table V), so that the value may not be very reliable. With the appearance of the first brood in the beginning of April, the weight rose rapidly, especially that of the Stage V Calanus, so that while the weight of 100 adult Calanus, male or female, rose from about 15 mg. on March 27th to 28 mg. on April 24th, 100 Stage V rose from 12 mg. to 37 mg. in the same time. After this, in accordance with size changes the weight of the females fell steadily to the end of May; it then rose to a secondary maximum in the middle of June, corresponding to the appearance of the second brood. There was a small rise in the beginning of July and another (corresponding to the beginning of the third brood) at



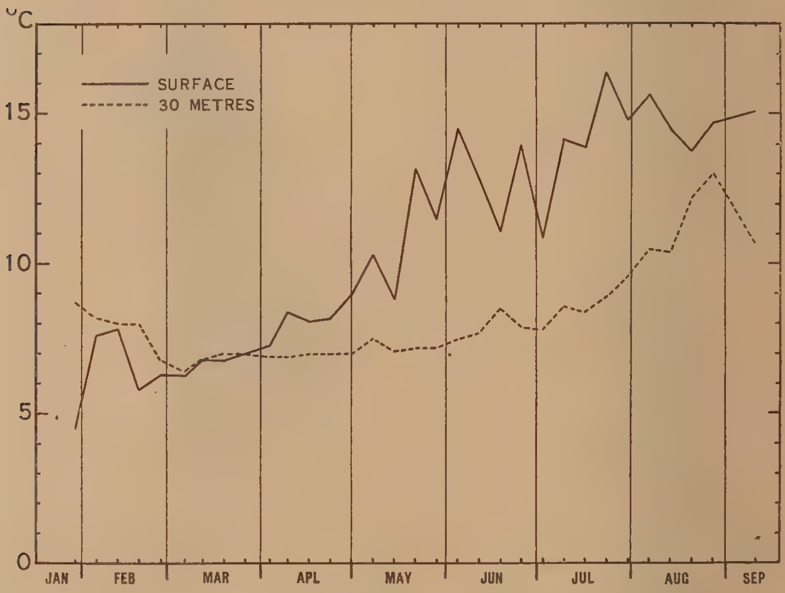
Text Fig. 3.—The median lengths of the copepodite stages of Calanus.

the end of July, but otherwise the weight fell gradually until winter values were reached again in September. The weight curve for males follows the size curve for males closely, with a maximum in June. Males were distinctly heavier than females throughout the summer. After the abrupt increase in weight in April Stage V Calanus remained heavier than either male or female for the rest of the summer, apart from several curious deviations in April and May, probably to be explained by imperfect sampling. The weight remained high until mid-July and then fell gradually till September, although even then it was still above winter values.



Text-Fig. 4.—Changes in median length and dry weight of 100 Calanus during the year. A, dry weight. B, median length. — — — Males; ———— Females; - - - - - Stage V.

The most striking point is, of course, that the relation of size to weight in female, male, and Stage V Calanus is *inverse*. It is obvious, therefore, that when a Stage V Calanus moults there must, at least during the summer, be a subsequent loss of organic material. It should be noted that the weights referred to above are all dry weights, and the same results do not hold if we compare wet weights. The wet weights of a number of male, female, and Stage V Calanus were determined on two occasions during the summer. About 50 Calanus were put in small drops of sea-water on a slide and the sea-water removed by carefully drying with filter paper. They were weighed after a fixed time, dried at 110° C., and reweighed. The dry weight of 100 individuals, determined in the usual way, acted as a check on this and showed that the adherent sea-water had been almost completely removed by the filter paper. It was found that while Stage V Calanus contained 47 to 50% water, male Calanus had 54% and females 68 to 70%. Thus in the living state females actually weigh more than males, and males more than Stage V. Gardiner (1933) has shown that large Calanus sink more quickly than small, indicating that females have a higher specific gravity than Stage V in spite of their lower dry weight.



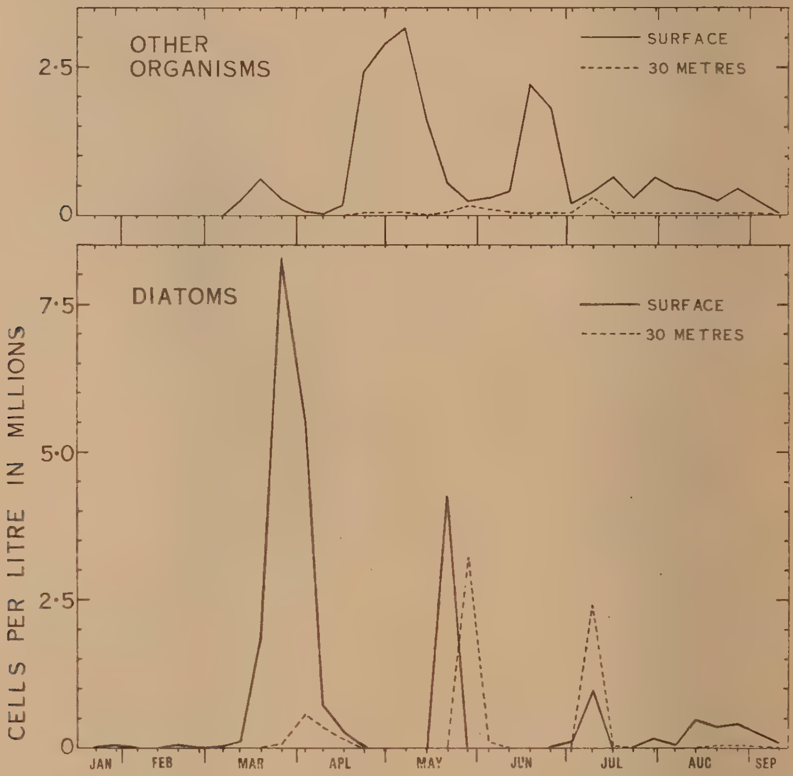
Text-Fig. 5.—The sea temperatures at the surface and 30 metres.

Throughout the year there is no constant relation between size and weight for male, female, or Stage V Calanus. In duplicate samples the agreement is good, but Calanus of the same stage and size show differences in dry weight at different times of the year which lie far beyond the experimental error of weighing or measuring. Thus of two lots of 100 Stage V Calanus with a median length of 2·35 mm. the first, on April 10th, weighed 23·0 mg., and the second, on July 24th, weighed 31·7 mg., a difference of 8·7 mg. As has been mentioned, however, the trend of the size and weight curves is similar throughout.

The temperatures taken are shown in Text-figure 5. The sea was coldest during March and April when the first brood, giving rise to the largest Calanus, was developing. Thereafter, concurrently with the warming of the sea-water, the later broods decreased in size. On this gradual fall in size are superimposed the variations caused by each brood. The Calanus found in January, February, and March were small, but these had developed from eggs laid in the previous autumn when the sea was at its warmest. Although it appears that the time taken to develop is about one month for each of the broods yet weekly visits cannot give an accurate figure for time of development which may on account of temperature be a little more for the first brood and a little less for the later ones.

RELATION TO THE PHYTOPLANKTON.

The water samples taken weekly at the surface and 30 metres were not preserved, but 20 c.c. were centrifuged from each within 24 hours and all the organisms counted. The numbers, expressed as millions per litre, are shown in Text-figure 6 (see Table IV). Apart from minute flagellates, diatoms were the only organisms occurring in large numbers and the cycle of events was very much the same as is usual in this area, namely, a large diatom increase in spring followed by smaller increases during the summer. The main difference was in the actual numbers present which, for the spring increase at least, were much smaller than in the years from 1926 to 1931 (diatoms were not counted in 1929). The maximum number during the spring increase in these years varied from 15 to 30 million cells per litre ; in 1932, although water samples were not taken regularly, there was apparently no great increase at all, and in 1933 the maximum number was only 8·5 million cells per litre. The summer increases were also small and the year as a whole must be considered poor in diatom growth. The majority of the other organisms (Table IV and Text-figure 6) were minute flagellates which occurred in large numbers during the summer. It is possible that these flagellates are characteristic only of coastal water and would not be found in such numbers in the open sea. Many of them are colourless. Dinoflagellates did not occur in large numbers. Samples taken at only two depths can give but a general idea of the total numbers present, and there may sometimes have been more than the curves indicate. On July 3rd, for instance, the numbers counted were not particularly large at either the surface or 30 metres, but the tow-netting from 10 metres to the surface was very rich in diatoms, indicating that the maximum (which must have been greater than the figures shown at 30 metres in the following week) was a little below the surface.



Text-Fig. 6.—The microplankton in Loch Striven in 1933.

Previous work (Lebour, 1922; Marshall, 1924) has shown that diatoms form an important part of the food of Calanus throughout the year and it might therefore be expected that the number of Calanus would bear some relation to the distribution of diatoms.

The spring increase this year, which lasted from March 13th to the middle of April, began at the time when the number of eggs was near its maximum and lasted over the period when the nauplii and young stages were developing (Plate I, Text-figure 1). These went through successfully to adults. The end of this increase overlapped the abortive beginning of the second brood which failed to produce more than a few survivors (Text-figure 1). Only the nauplii from the eggs spawned during the first few days of this production had a sufficient food supply. There was a large number of minute flagellates present during this time but they had no effect on the survival.

The second diatom increase, at the end of May, coincided with the appearance of the second brood, but did not last so long. Similarly the increase from July 3rd to 10th provided diatoms when the eggs and nauplii of the first part of the third brood were at their maximum, and these gave rise to the main bulk of the copepodite stages of this brood. Diatoms were very scarce again until July 31st, and this is reflected in the lack of nauplii from the eggs produced at the end of this brood (Plate I). Throughout August and September there was a small number of diatoms constantly present, which may have been responsible for the survival of the subsidiary fourth brood, but by this time most of the developing Calanus were not moulting into adults but remained as Stage V to form the autumn–winter stock.

Earlier work has shown that a large percentage of the diatoms produced during an increase sink to the bottom. Since the Calanus of the first brood were found almost entirely in the upper layers (Text-figure 2) the diatoms when they had sunk into deep water were of no significance to them. With the second and third broods the diatoms would be of value to the young stages when they were near the surface and in deeper water would be available for the older stages. It is curious to note that the minute flagellates, although they would appear to be suitable food, do not seem to be used.

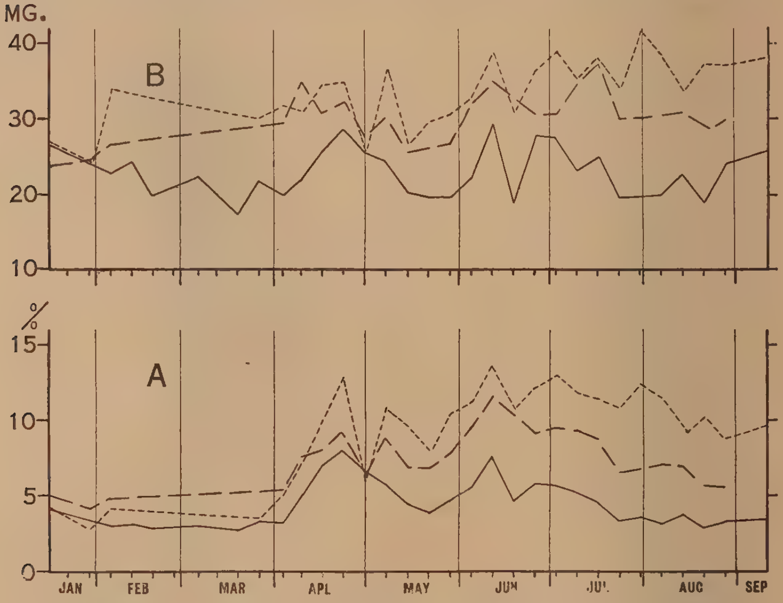
It is, of course, impossible to state what are the actual requirements of a Calanus, but the young stages, being less mobile, will require a richer supply than the later stages and adults. The critical time is therefore the period from egg to early copepodite, and the presence or absence of diatoms in the water then, means the success or failure of a brood.

The coincidence of a diatom increase with egg production (except in the case of the abortive beginning to the second brood) is interesting, but no causal relation is apparent.

In Text-figure 3 the periods when there were over 100,000 diatom cells per litre are marked in black. It can be seen that the size maxima occur shortly after these diatom-rich periods. The size maxima depend mainly on the broods, but it is possible that a rich food supply may also have a direct effect on the size.

Chemical Composition.

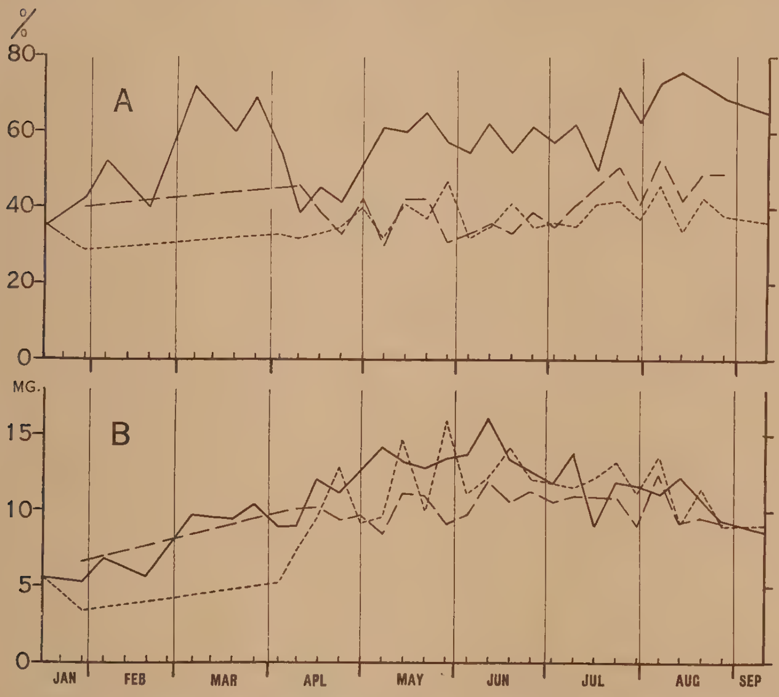
The fat and protein content was estimated from January to September in male, female, and Stage V Calanus. The methods used were the same as described in Part IV, but during 1933 the Calanus were not measured. The samples used for fat and protein analyses could not conveniently be weighed, so that the assumption is made that the samples of 100 Calanus used for these were strictly comparable with those used for weight and size determination. That this is justified is shown by the agreement between the duplicate weight samples and between the curves for weight and fat content.



Text-Fig. 7.—Changes in fat content of Calanus during the year. A, Fat percentage. B, Weight of fat per 100 Calanus. — — — Males; ———— Females; - - - - - Stage V.

The weight of fat per 100 Calanus and the percentage of fat are shown in Text-figure 7. In the early part of the year male and Stage V Calanus were scarce and it was often difficult to get sufficient for analysis. Corresponding with the low values for weight at this time of year fat content was also low. With the appearance in April of the Stage V and adult Calanus of the first brood there was a rapid increase in fat content; thereafter the curves showing fat content of male and female Calanus agree well throughout with weight and size (Text-figure 4), while that for

Stage V shows a very good agreement except for a short period during July. Thus with male and female Calanus the three broods for the year can be recognised by the change in fat content. With Stage V, as has already been mentioned, the sampling errors are at times significant and the curve for fat content follows that for weight, which has considerable irregularities during the spring. Both the actual content and percentage of fat are lowest in females and highest in Stage V, in agreement with weight. There is a maximum fluctuation in percentage of fat in male Calanus of 20%, in females of 13%, and in Stage V of 20%. While the curves show that the large increase in the actual fat content in April depends chiefly on the increase in weight, Text-figure 7A shows that the increases in the *percentage* of fat occur at the same time and are therefore related to broods. This is shown most clearly for the first brood of the year, less clearly for the second, and still less for the third, as was the case with sizes. These increases in the percentage of fat suggest that the abundant food provided by the spring diatom increase resulted in a storage of fat.



TEXT-FIG. 8.—Changes in protein content of Calanus during the year. A, Protein percentage. B, Weight of protein per 100 Calanus. — — — Males ; ———— Females ; - - - - - Stage V.

After the appearance of the third brood there is a general fall in the fat contents of male and female Calanus, which by September have reached approximately the same values as in early spring. The adults then die out. With Stage V, however, the value is still high in the autumn–winter stock in September, being about 6% higher than during the spring.

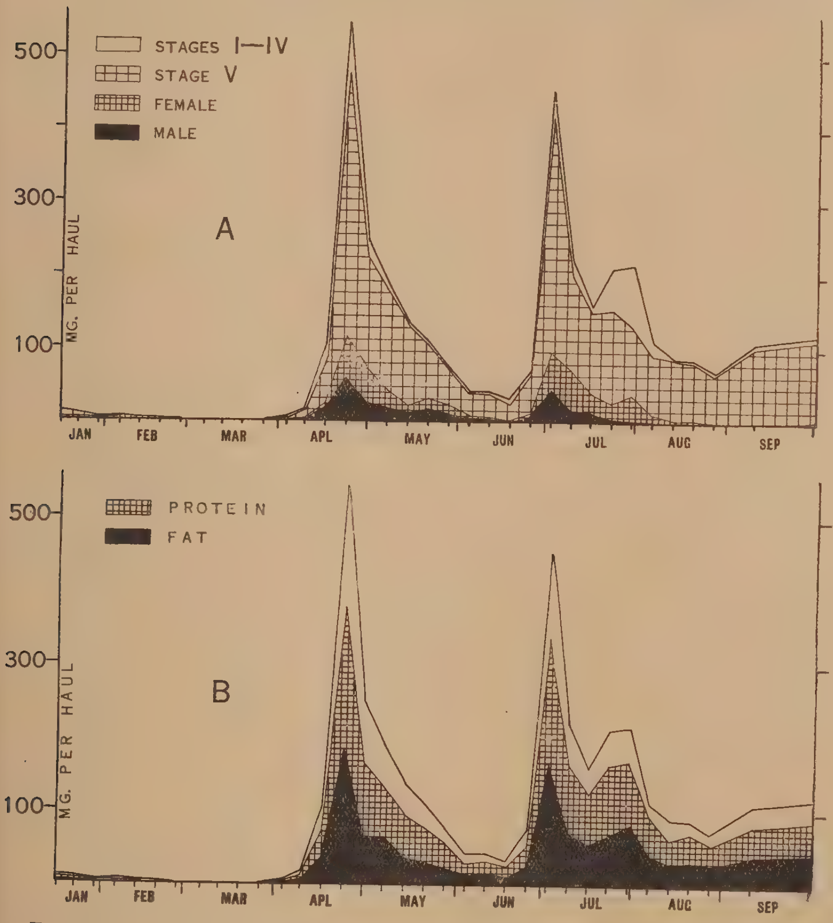
There is little or no relation shown between the fat content of female Calanus and the state of the ovaries. As is shown in Table V, there was always a high percentage of those in the mature condition, so that any changes due to the variations in this must be small and would not be shown in the curves for fat content.

The protein content of Calanus and the protein percentage are shown in Text-figure 8. There is less agreement between weight and protein than between weight and fat content. This is partly because the method of analysis was less accurate, and also because protein was estimated less frequently than fat. The agreement between protein content and weight is shown in the rise to higher values in April corresponding to the first brood, especially in Stage V. During the summer the values remained high and showed at best only a general relation to weight. After the third breeding period in July there was a fall towards winter values again. Text-figure 8B shows that, in contrast to fat, females are richest in protein and Stage V poorest. In the case of protein the difference between females on the one hand and males and Stage V Calanus on the other is more marked than with fat. The curves for protein percentage do not show any relation to the breeding periods with the possible exception of females, and their chief feature is a comparative constancy in male and Stage V Calanus. Thus the great increase of weight in spring is due more to fat than to protein.

On the basis of the weight, fat, and protein determinations, diagrams showing the total dry weight of the copepodite stages and the amount of fat and protein per haul have been constructed (Text-figure 9). The dry weights of the early copepodite stages have been calculated on the basis of Bogorov's figures (1933), while nauplius stages and eggs have been omitted, since although they were at times present in large numbers, their weight will be insignificant in comparison with copepodites and adults. During the winter the total weight (Text-figure 9A) was low because of the small numbers. The increase in the middle of April corresponded to the appearance of copepodites from the first brood. Those from the second brood, in May, caused the second weight peak on July 3rd. The third brood caused a slight increase on July 24th and 31st in which the early copepodites were of considerable importance. Thereafter the curve remained high owing chiefly to the Stage V Calanus which formed the autumn–winter stock.

The fat and protein content and the unidentified constituents of the

Calanus as a whole (Text-figure 9B) follow fairly closely the total weight curve. Of the unidentified constituents ash amounts to about 4% and chitin to about 3% (see Part IV) of the dry weight of the Calanus, while the remainder is probably largely carbohydrate (Brandt, 1898; Brandt and Raben, 1919–1922). At its maximum on April 24th the total dry weight of the copepodite stages was over 540 mg. in the whole column of water filtered (about 70 metres). This corresponds to a concentration of about 40 mg. per cubic metre, but the actual concentration will of course depend entirely on the vertical distribution of the Calanus.



Text-Fig. 9.—Diagram showing dry weight of Calanus per haul. A, Relative weights of different copepodite stages. B, Fat and protein content.

NOTES ON PARASITES.

A striking fact about Calanus is the number found parasitised. Apstein (1911) has already given a list of parasites which occur, and it may be of interest to add a few notes on those found here and their distribution.

Parasitised forms are often recognisable by their colour. Those whose body cavities contain cestode larvæ, trematodes, or dinoflagellates are all coloured red. With cestodes and trematodes the colour seems to be a development of the red pigment present in the chromatophores usually associated with the fat body, and the whole animal may be coloured a brilliant scarlet. In those parasitised with dinoflagellates the colour is associated with the mass of the parasites and varies from a pinkish yellow to bright red. The other parasites do not affect the colour at all.

An isopod of the genus Microniscus occurs occasionally throughout the year.

Two types of cestode larvæ are found, a tetraphyllid and a cyclophyllid. Both occur in large numbers in the body cavity, the cyclophyllid being smaller and more numerous. Apstein has recorded over 2000 of them in one Calanus, but the numbers here have not been more than several hundred. When these parasites were first noticed in this area, about 1924, they were rare, the tetraphyllids much rarer than the cyclophyllids. By about 1930, however, the tetraphyllids had become more numerous and in 1932 and 1933 cyclophyllids were exceedingly rare and tetraphyllids comparatively common. An interesting point about these cestode larvæ is of course the difficulty of explaining how they can occur in such large numbers in a single host.

Trematodes, probably a species of Hemiurus, occur rarely and are found only singly. The most brilliantly coloured Calanus are usually those which contain a trematode. They have also been found in Pseudocalanus.

Nematodes also occur singly in the body cavity but have no effect on the colour. They may be very small, but all sizes are found up to those which are longer than the Calanus which contains them and lie coiled up in the body cavity. These were rare until the spring of 1933, when they became comparatively common. Dr. Baylis has kindly identified this form as Contracæcum sp. At the same time this species was also common in Sagitta.

A species of gregarine is frequent in the gut and is more common in summer than in winter. It appears to have no effect on the Calanus at all.

The most common parasite of all is a species of the dinoflagellate Syndinium which occurs in masses in the body cavity. When such parasitised Calanus are kept in the laboratory they will frequently extrude the parasites as a discrete mass, but the host usually dies soon afterwards. Rarely, they extrude a mass of flagellated swarm-spores. The number of Calanus parasitised by this form is so large that it probably has a considerable effect on the mortality. The Calanus infected are usually found swimming about actively, but they are less resistant than normal specimens and die more quickly in the laboratory.

Another parasite, probably also a dinoflagellate, is *Ellobiopsis chattoni*, which is a pear-shaped body attached by a stalk usually to the antennule or one of the other cephalic appendages. It occurs most frequently in summer and was very common in the summers of 1931 and 1932. It was rare in 1933.

Except for the Syndinium, none of these parasites has much apparent effect on Calanus, which remain as active and lively as normal specimens. If they are examined more closely, however, it is usually found that the ovary remains undeveloped in females containing trematodes, cestodes, nematodes, or Syndinium. Females are found parasitised much more frequently than any other stage. Syndinium is found often in Stage V and sometimes in male Calanus, and the same may be said of nematodes and Ellobiopsis, but it is rare to find cestodes or trematodes in any but adult females.

On the whole infection is much heavier in the autumn–winter stock than in any other. These Calanus have lived much longer than those of other broods and have therefore been exposed to infection for a longer time. It is curious to notice the change which comes with the appearance of the first brood. Whereas out of a catch of a few hundred of the autumn–winter stock there may be 50 or 60 infected Calanus, out of the much larger catches of the first brood it is rare to find more than a dozen parasitised. In a catch taken on March 26th, 1931, out of 363 females, 42 were infected with Syndinium, 27 with tetraphyllids, 3 with cyclophillids, 6 with nematodes, and 1 with Ellobiopsis. Infection such as this probably accounts for a heavy mortality.

DISCUSSION.

A comparison with last year's results (Part I) shows that in general there is close agreement. The three main breeding periods, with one or more subsidiary broods, found at all Stations last year, were repeated in Loch Striven. The abortive beginning of the second brood and the accumulation of Stage V after the first brood delayed both the second and third broods by about a month, so that the autumn–winter stock was not established until August 14th (compared with July 11th in 1932). It is considered therefore that this may be regarded as a true representation of the course of breeding in the Clyde Sea-Area.

If total numbers are considered alone (Plate I) three distinct peaks appear which, except for the first, are caused mainly by large numbers of eggs. The eggs in the first are those of the abortive beginning of the second brood while the copepodites are those from the first brood, the eggs of which appeared in February and March, but were found in relatively small numbers. It has been shown that diatoms coincided with the eggs and nauplii of each brood and so aided their survival, but this will also have affected the number caught, since when diatoms are thick considerable clogging of the net is caused and its fishing capacity largely reduced. This was observed on several occasions, when the net on reaching the surface was seen to be pushing a cushion of water in front of it, and as it was hauled out brought water with it which drained away more or less slowly. This did not happen except when diatoms were very numerous. Thus while an inaccurate sample of the eggs and nauplii might have been taken because of diatoms, by the time they had developed into older copepodites diatoms had disappeared and truer samples were obtained. This applies in general to the later broods, but less to the third, since the number of diatoms at this time probably did not reach such high values as in the two preceding increases.

In the third brood alone were young stages present in sufficient numbers to produce the later copepodites and adults, and a diminution is shown from each stage to the next throughout this brood (except the first copepodites whose peak in numbers may have been missed between two successive weekly visits). In the first and second broods the reverse was the case, there being an actual increase in numbers from one stage to the next, but, as has been shown, this follows the increased efficiency of the net with decrease in diatoms. A similar state of affairs has been ascribed by Gibbons (1933) in the North Sea to immigration. It is, however, very difficult to apply this to Loch Striven. Text-figure 1 shows clearly that no large immigration of any particular stage took place at any time during the year. The broods can be followed in successive weeks from egg up to adult without any break in continuity. Apart from this it is known from previous work that hydrographic conditions in Loch Striven show no violent changes and that the microplankton maintains a more or less independent character, although the same general changes take place there as in the rest of the area.

The resemblances between the course of events in this and other areas have already been pointed out (Part I). Off the south coast of Ireland (Farran, 1927) the first brood appears to be so small that the copepodites resulting from it are negligible in numbers; the second brood in April and May is important and Farran states that thereafter breeding is continuous throughout the summer. His work, however, is based on collections accumulated over a number of years (1913–14 and 1920–26) and data for more than two consecutive months in any year were not obtained. They cannot, therefore, be expected to show distinct broods since these may occur at different times in different years. The recently published work of Gibbons in the North Sea (1933) does not give sufficient data for a comparison to be made. He states, however, that two broods occur, the main one in April and a secondary one in August.

On page 806 it has been shown that the phytoplankton had an effect on Calanus in 1933, mainly on the survival of the broods. In 1932 this connexion was not so obvious. There were then diatoms present during at least part of each spawning period at Stations I and II so that no brood failed completely for lack of food. At Station IV there was only one diatom increase, during May and June, which accounted for the survival of the second and third broods, but did not provide food for the first brood in March which failed. It is interesting to compare the delay in the start of breeding in Loch Fyne in 1932 and the accumulation of Stage V before the second brood in Loch Striven with the absence of diatoms in both cases.

In the open sea diatoms are less numerous than in the Clyde Sea-Area, and as a rule there is a large outburst of growth in spring and a smaller one in autumn (Gran, 1929). The sporadic increases during the summer which occur in the Clyde Sea-Area are absent. It is possible that this may have an effect on the Calanus population by delaying, or at least diminishing, one of the later broods.

In fresh water a relationship between the maxima of Cladocera and those of the phytoplankton has been shown by Krogh and Berg (1931).

It is clear that once breeding starts Calanus takes about a month to develop from egg to adult. The eggs appear after two to four weeks, spawning may last for several weeks, and the adults then die out. This sequence of events results in the production of successive broods during the summer, but owing to differences in survival these may not be apparent when only copepodites are taken into account.

The size curves show very much the same features as in 1932. They are seldom clearly unimodal except at the appearance of a new brood (Plate II, April 10th, July 31st). The Stage V and females have a particularly wide range. Although in 1933 the maxima in size correspond with diatom increases the connexion is probably indirect, for in 1932, although in several cases peaks in size corresponded with peaks in diatoms (Part II, p. 122) yet during the longest continued diatom increase there occurred a size minimum as well as a size maximum. In 1932 the connexion between broods and size was shown most clearly in females and Stage V at Station I. In 1933 it is not so clear and shows mainly in females and young copepodites.

The Stage V Calanus in Loch Striven had a considerably larger range in weight than those from Loch Fyne in 1932 (Part IV). In both cases the lowest values (10–12 mg.) were obtained in spring when numbers were low. Loch Fyne was peculiar in that there was no diatom increase until May and that the first brood was delayed and was unsuccessful. It was probably on account of this that the numbers and weight fell steadily till May and the sudden increase in weight came with the second and not with the first brood. After this the females remained much lighter than Stage V in spite of their greater size, as in 1933. The maximum weight of Stage V for the year was considerably higher in Loch Striven (37 mg. on April 24th) than in Loch Fyne (28 mg. on December 14th, 1931). The values for fat and protein percentage were comparable with those for Loch Fyne though the range was greater there. Females had low fat and high protein percentages compared with Stage V, while males occupied an intermediate position. Owing to the comparatively small numbers of analyses made in 1932, the seasonal cycle was not so well shown in Loch Fyne.

The curves for total weight per haul are very different in the two cases except for the low weights in spring. The stock of Stage V Calanus present in Loch Fyne in the winter of 1931–32 was very high when compared with the 1932–33 autumn–winter stock in Loch Striven. With the onset of breeding in spring, the total weights rose in both lochs, corresponding with the number of copepodites.

SUMMARY.

1. The seasonal changes in the population of Calanus in Loch Striven in 1933 have been investigated.

2. There were three main breeding periods. The first was in February and March, an unsuccessful beginning of the second in April, the true second brood in May to June, the third in July, and subsidiary broods in August and September.

3. Numbers were very low until April when the copepodites of the first brood caused a large increase ; there was a second increase in May consisting mainly of the eggs of the second brood, and the maximum for the year came in July. The last and subsidiary broods provided the stock for the autumn and winter of 1933.

4. The reliability of the total numbers is discussed and it is concluded that a study of the percentage composition of the catch gives a reliable indication of the course of breeding.

5. A breeding period is always preceded by a large proportion of females with immature ovaries which gives way to a large proportion of mature females at the time of spawning. Spermatophores are found

chiefly on females with immature ovaries and are usually most numerous when males are abundant.

6. The Calanus of the first brood were almost entirely restricted to the upper 10 metres. This was not so for Stage V and adults of the later broods.

7. The Calanus of the first brood, which developed when the sea was at its coldest, were the largest found during the year. Thereafter there was a gradual fall, corresponding to the warming of the sea. On this fall was superimposed a series of variations caused by each brood. With the first appearance of each brood the fall in size was temporarily checked. This is shown for each copepodite stage.

8. The changes in dry weight followed the broods and changes in size, the most marked change being with the first brood in April, after which there was a general fall. Females, though largest, weighed least and Stage V, though smallest, were heaviest. This is due to differences in water content.

9. There was a spring diatom increase in March-April, followed by smaller increases in May, July and August-September. These coincided with the three main spawning periods so that the resulting nauplii had a rich food supply. The eggs spawned in April lacked diatoms and failed to develop into copepodites. The results indicate that the success or failure of a brood depends on the presence or absence of diatoms during the early stages of development.

10. The remaining constituents of the microplankton (chiefly minute flagellates) although at times numerous show no relation to breeding periods or survival.

11. The fat content of Calanus followed the changes in weight. There was also an increase in the percentage of fat with the appearance of each brood. The percentage of fat was highest in Stage V and lowest in females.

12. The protein content of Calanus followed in general the changes in weight. The percentage of protein was highest in females and lowest in Stage V.

13. The increase in percentage of fat which accompanied the increase in size and weight with the appearance of each brood suggests that a storage of fat can take place when food is plentiful.

14. The total weight of Calanus per haul is largely dependent on the number of Stage V copepodites.

15. The parasites occurring in Calanus are considered. They are most abundant in the females from the autumn–winter stock.

16. A comparison is made with previous work in this and other areas.

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TABLE I.

Calanus in Five Hauls.

Date.		Eggs.		Nauplii.		Copepodites.										Adults.				Total.
						I.		II.		III.		IV.		V.		♀		♂		
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Jan.	17	–	–	2	1	–	–	–	–	–	–	1	–	223	73	57	19	22	7	305
,,	23	–	–	–	–	–	–	–	–	–	–	–	–	166	67	54	22	28	11	248
,,	30	3	2	–	–	–	–	–	–	–	–	1	1	104	65	30	19	21	13	159
Feb.	6	2	1	–	–	–	–	–	–	–	–	–	–	76	31	151	61	20	8	249
,,	13	7	5	7	5	–	–	–	–	–	–	–	–	46	33	69	50	10	7	139
,,	20	34	32	19	18	–	–	–	–	–	–	–	–	3	3	50	47	1	1	107
,,	27	13	28	23	49	1	2	–	–	–	–	–	–	3	6	7	15	–	–	47
March	7	83	59	18	13	1	1	–	–	–	–	–	–	2	1	36	26	1	1	141
,,	13	53	64	20	24	1	1	–	–	–	–	–	–	–	–	9	11	–	–	83
,,	20	79	42	39	21	23	12	31	16	6	3	–	–	1	1	11	6	–	–	190
,,	27	2	1	49	32	35	23	15	10	23	15	18	12	3	2	7	5	1	1	153
April	4	9	1	55	5	114	11	262	26	339	33	120	12	113	11	9	1	5	1	1,026
,,	10	387	32	99	8	49	4	104	9	123	10	167	14	174	14	39	3	63	5	1,205
,,	17	2,508	40	325	5	298	5	562	9	504	8	457	7	1,091	18	115	2	349	6	6,209
,,	24*	3,215	29	215	2	95	1	150	1	435	4	1,270	12	3,925	36	815	7	835	8	10,955
May	1	329	5	84	1	74	1	257	4	314	5	819	12	3,232	48	1,014	15	555	8	6,678
,,	8*	256	8	8	–	24	1	92	3	96	3	212	7	1,808	57	428	14	256	8	3,180
,,	15†	243	20	27	2	4	–	26	2	62	5	42	4	591	50	105	9	95	8	1,195
,,	22*	7,015	70	1,155	12	5	–	–	–	30	–	135	1	1,065	11	270	3	295	3	9,970
,,	29	4,168	64	1,120	17	2	–	10	–	11	–	22	–	733	11	279	4	190	3	6,535
June	5*	1,692	48	1,124	32	124	4	66	2	48	1	24	1	364	10	40	1	83	2	3,565
,,	12†	786	45	474	27	112	6	64	4	61	4	29	2	169	10	28	2	31	2	1,754
,,	19*	276	21	94	7	108	8	223	17	179	14	121	9	256	20	28	2	14	1	1,299
,,	26*	447	28	67	4	30	2	18	1	58	4	116	7	646	40	154	10	79	5	1,615
July	3*	1,910	23	180	2	40	1	30	–	140	2	400	5	3,900	48	970	12	585	7	8,155
,,	10*	25,080	68	8,310	23	180	1	85	–	165	–	410	1	1,535	4	985	3	250	1	37,000
,,	17	2,350	28	1,576	19	538	6	671	8	382	5	153	2	1,692	20	726	9	302	4	8,390
,,	24	21,516	66	776	2	709	2	2,709	8	3,225	10	983	3	2,016	6	607	2	150	1	32,691
,,	31	389	4	785	9	683	8	666	7	1,670	19	2,279	25	1,550	17	936	10	72	1	9,030
August	7	1,304	28	489	11	94	2	214	5	254	6	584	13	1,343	29	278	6	52	1	4,612
,,	14	93	5	26	1	8	–	36	2	15	1	105	6	1,540	81	35	2	42	2	1,900
,,	21	25	1	9	1	21	1	81	4	62	3	95	5	1,468	80	60	3	24	1	1,845
,,	28†	8	1	–	–	28	4	67	8	50	6	83	10	543	68	15	2	7	1	801
Sept.	11	112	4	–	–	12	1	–	–	60	2	228	9	1,996	79	96	4	24	1	2,528
Oct.	2‡	5	1	1	–	1	–	1	–	18	3	49	8	478	81	36	6	3	1	592

* Numbers in 4 hauls. † Numbers in 2 hauls. ‡ Numbers in 1 haul.

TABLE II.

NUMBER OF CALANUS ABOVE AND BELOW 10 METRES IN THE DIVIDED HAUL.

Date.	Below 10 metres.									Above 10 metres.									
	Eggs.	Npl.	I.	II.	III.	IV.	V.	♀	♂	Eggs.	Npl.	I.	II.	III.	IV.	V.	♀	♂	Total.
March 27	–	1	–	1	–	–	–	–	–	1	16	13	4	3	–	1	–	–	40
April 4	–	2	1	3	8	3	13	1	2	4	18	20	61	105	31	18	1	–	291
,, 10	3	3	1	4	4	8	16	3	3	114	7	7	13	24	40	15	1	–	266
,, 17	36	8	5	3	4	8	32	5	22	480	17	45	111	128	97	63	6	15	1,085
,, 24*	224	13	1	1	1	37	164	63	46	27	2	4	26	64	88	85	8	39	893
May 1	64	19	14	21	18	84	612	197	93	–	–	–	11	71	170	140	12	17	1,543
,, 8*	79	24	–	1	1	2	33	5	3	7	1	5	19	43	65	80	21	27	416
,, 15*	19	8	–	–	1	1	11	2	6	1	–	–	6	16	4	13	8	5	101
,, 22*	81	17	–	–	–	–	25	2	18	2,915	220	1	1	–	7	4	12	5	3,308
,, 29	241	102	–	1	–	–	86	22	27	407	82	2	1	3	2	11	5	3	995
June 5*	37	97	2	1	1	1	32	1	3	4	198	18	1	–	–	–	–	–	396
,, 12	250	103	6	2	4	4	43	1	9	31	63	73	43	31	8	1	–	–	672
,, 19*	36	19	–	3	3	5	50	4	–	4	7	38	73	37	18	–	1	–	298
,, 26*	25	8	1	3	2	3	48	11	8	203	12	–	–	1	–	1	–	–	326
July 3*	22	2	3	10	18	43	529	101	103	577	15	–	–	–	–	1	–	1	1,425
,, 10*	262	309	32	43	45	80	261	221	48	277	50	1	–	–	–	–	1	–	1,630
,, 17	317	274	162	241	177	63	337	221	57	38	2	1	–	–	–	–	–	–	1,890
,, 24	935	104	88	209	254	101	301	57	19	931	2	1	–	1	2	5	–	1	3,011
,, 31	35	90	100	85	140	167	218	132	12	42	7	3	1	2	–	–	–	–	1,034
August 7	65	45	4	26	22	80	152	38	4	23	24	2	–	–	–	3	–	–	488
,, 14	13	2	–	2	1	3	103	3	2	10	2	–	–	–	–	3	–	–	144
,, 21	8	2	1	22	16	13	202	8	6	3	1	2	1	–	–	2	–	–	287

* This haul excluded from Table I.

TABLE III.

MEDIAN LENGTHS OF CALANUS IN 1933.

	Males.		Females.		Stage V.		Stage IV.		Stage III.		Stage II.		Stage I.	
Date.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.
17.1.33	20	2·53	58	2·56	212	2·10	—	—	—	—	—	—	—	—
23.1.33	26	2·44	55	2·56	161	2·08	—	—	—	—	—	—	—	—
30.1.33	149	2·34	98	2·41	99	2·05	—	—	—	—	—	—	—	—
6.2.33	79	2·40	593	2·40	76	2·08	—	—	—	—	—	—	—	—
13.2.33	38	2·34	184	2·41	41	2·00	—	—	—	—	—	—	—	—
20.2.33	12	2·36	217	2·45	—	—	—	—	—	—	—	—	—	—
27.2.33	—	—	25	2·50	—	—	—	—	—	—	—	—	—	—
7.3.33	—	—	71	2·40	—	—	—	—	—	—	—	—	—	—
13.3.33	—	—	27	2·36	—	—	—	—	—	—	—	—	—	—
20.3.33	—	—	86	2·48	—	—	—	—	—	—	28	1·03	22	0·74
27.3.33	—	—	68	2·41	—	—	15	1·76	23	1·43	13	1·06	29	0·73
4.4.33	72	2·44	100	2·58	105	2·30	116	1·87	113	1·48	106	1·09	87	0·76
10.4.33	175	2·50	224	2·70	146	2·40	140	1·93	111	1·51	91	1·07	44	0·73
17.4.33	101	2·58	137	2·79	197	2·49	102	1·98	123	1·50	113	1·06	106	0·74
24.4.33	152	2·61	151	2·82	174	2·49	96	1·95	81	1·46	52	1·03	87	0·71
1.5.33	78	2·62	148	2·80	195	2·48	93	1·89	125	1·42	74	1·03	26	0·69
8.5.33	85	2·60	118	2·78	165	2·45	105	1·85	68	1·38	41	0·98	—	—
15.5.33	101	2·62	144	2·74	160	2·51	74	1·75	75	1·33	33	0·96	—	—
22.5.33	168	2·61	149	2·71	189	2·51	103	1·76	31	1·36	—	—	—	—
29.5.33	141	2·63	139	2·65	141	2·49	24	1·79	—	—	—	—	—	—
5.6.33	82	2·67	39	2·66	253	2·50	25	1·81	48	1·42	63	0·99	120	0·66
12.6.33	186	2·64	169	2·66	146	2·42	45	1·74	71	1·33	68	0·94	104	0·64
19.6.33	178	2·61	186	2·65	182	2·44	101	1·73	119	1·28	113	0·90	105	0·63
26.6.33	138	2·54	139	2·58	150	2·35	107	1·71	58	1·33	21	0·95	30	0·66
3.7.33	116	2·57	184	2·51	185	2·40	118	1·74	102	1·29	70	0·95	84	0·68
10.7.33	95	2·52	196	2·45	251	2·35	162	1·75	76	1·34	58	0·97	62	0·68
17.7.33	100	2·43	207	2·46	232	2·33	77	1·76	111	1·28	133	0·94	125	0·63
24.7.33	139	2·41	107	2·41	295	2·33	97	1·68	119	1·25	106	0·91	140	0·64
31.7.33	118	2·43	131	2·42	211	2·34	163	1·59	136	1·23	84	0·91	101	0·64
7.8.33	59	2·47	97	2·41	290	2·22	106	1·58	78	1·23	72	0·90	82	0·64
14.8.33	40	2·39	33	2·35	233	2·33	83	1·65	—	—	—	—	—	—
21.8.33	19	2·46	47	2·30	194	2·35	71	1·67	54	1·26	89	0·94	22	0·67
28.8.33	—	—	14	2·36	240	2·30	78	1·62	50	1·24	61	0·93	28	0·63
11.9.33	19	2·35	104	2·23	247	2·25	202	1·61	46	1·24	—	—	—	—
2.10.33	—	—	34	2·27	235	2·17	46	1·68	17	1·28	—	—	—	—

TABLE IV.

NUMBER OF ORGANISMS IN 20 C.C. OF SEA WATER.

Date, 1933.	Depth in m.	All Diatoms.	Skeletonema.	Thalassiosira.	Leptocylindrus.	Rhizosolenia.	Chaetoceros.	Pennate Diatoms.	Other Diatoms.	Dinoflagellates.	Silicoflagellates.	Coccolithophores*	Unidentified flagellates.*	Ciliates.	Other organisms.	T. in °C.
23·1	0	165	125	10	—	—	24	4	2	2	3	—	61	2	1	—
23·1	30	33	9	6	—	—	—	14	4	1	—	—	1	—	1	—
30·1	0	707	673	11	—	—	—	23	—	4	3	—	210	—		4·50
30·1	30	25	5	5	—	—	—	26	6	6	—	—	6	—	1	8·70
6·2	0	LOST														7·63
6·2	30	22	6	11	—	—	—	11	2	7	—	—	10	—	—	8·20
13·2	0	102	66	16	—	—	—	14	6	2	—	—	8	—	—	7·80
13·2	30	36	15	5	—	—	2	13	1	7	—	—	5	—	—	8·04
20·2	0	876	809	20	—	—	8	36	3	20	—	—	260	1	—	5·80
20·2	30	36	8	8	—	—	—	20	—	2	—	—	4	1	1	7·95
27·2	0	245	142	58	—	—	3	42	—	6	—	—	26	1	1	6·32
27·2	30	334	239	35	—	—	—	58	2	5	—	—	7	1		6·81
7·3	0	490	365	56	—	—	7	60	2	7	—	—	51	1	1	6·32
7·3	30	355	204	80	—	—	1	70	—	1	—	—	4	—	—	6·37
13·3	0	2,048	1,794	219	—	—	23	12	—	23	—	—	5,200	9	—	6·83
13·3	30	139	89	16	—	—	—	34	—	3	—	—	39	—	—	6·82
20·3	0	37,200†	34,405	2,460	—	—	25	310	—	30	—	—	12,500	2	14	6·82
20·3	30	201	155	10	—	—	—	36	—	1	—	—	20	—	—	7·03
27·3	0	166,000†	123,800	41,450	—	—	375	375	—	29	8	90	5,300	2	9	7·02
27·3	30	822	732	67	—	—	8	15	—	—	—	—	10	1	—	7·00
4·4	0	111,000†	107,100	3,900	—	—	—	—	—	3	2	—	1,260	—	6	7·27
4·4	30	11,165	10,850	240	—	—	8	67	—	1	3	—	—	—		6·87
10·4	0	15,228	14,700	189	—	—	66	273	—	54	2	—	3,600	3	—	8·35
10·4	30	7,466	7,300	160	—	—	—	6	—	2	4	—	17	1	1	6·92
17·4	0	5,487	5,300	10	—	9	74	82	12	61	1	30	3,500	9	1	8·07
17·4	30	2,548	2,370	156	—	—	3	8	12	5	8	—	25	3	1	7·01
24·4	0	7	2	—	—	—	—	5	—	15	1	—	48,000		13	8·18
24·4	30	155	142	12	—	—	—	1	—	5	1	—	500	1	—	6·97
1·5	0	26	22	—	—	—	4	—	—	33	—	—	58,000	—	—	9·01

1·5	30	249	213	34	—	—	—	2	—	7	—	—	600		—	7·02
8·5	0	5	—	—		—	—	5	—	31	—	—	63,000	—	—	10·32
8·5	30	98	85	13	—	—	—	—	—	1	1		800	4	—	7·47
15·5	0	17	8	1	—	—	—	8	—	8	2	—	32,000		—	8·79
15·5	30	56	27	26	—	—	—	2	1	2	1	—	330	—	—	7·10
22·5	0§	85,000†	74,440	10,420	—	—	—	140	—	144	4	—	11,000	4	202	13·15
22·5	30	64	49	12	—	—	2	1	—	2	—	—	700	2	—	7·22
29·5	0	65	37	8	20	—	—	—	—	72	—	30	5,000	—	2	11·45
29·5	30	64,000†	60,660	3,215	—	—	—	125	—	8	133	—	3,000	6	—	7·20
5·6	0	19	15	1	—	—	3	—	—	91	—	—	6,000	1	9	14·51
5·6	30	2,220	1,915	292	—	—	—	13	—	4	6	—	2,000	2	1	7·53
12·6	0	2	—	2	—	—	—	—	—	50	—	—	8,000	—	2	12·90
12·6	30	96	83	9	—	—	—	3	1	9	7	—	1,000	—	2	7·71
19·6	0	26	22	2	—	—	—	2	—	31	—	100	44,000	—	1	11·10
19·6	30	59	32	26	—	—	—	1	—	6	4	100	900	—	1	8·51
26·6	0	104	2	—	96	—	3	3	—	151	1	1,400	34,600	1	2	14·04
26·6	30															7·90
3·7	0	2,167	1,761	173	29	1	16	187	—	20	1	150	4,000	—	—	10·93
3·7	30	64	45	17	—	—	—	2	—	5	1	—	600	3	1	7·78
10·7	0	19,571	45	43	19,200†	8	176	95	4	209	—	500	7,600	1	10	14·06
10·7	30	48,000†	42,780	1,370	385	—	1,240	2,225	—	1	6	300	5,700	4	—	8·63
17·7	0	107	7	11	2	1	53	33	—	73	72	600	12,400	4	1	13·90
17·7	30	555	296	153	6	—	11	89	—	6	2	30	600	—	—	8·42
24·7	0	40	4	—	17	2	8	9	—	64	—	100	6,000	3	—	16·40
24·7	30	181	77	80	—	—	6	18	—	12	1	30	700	1	—	8·90
31·7	0	3,288	3	14	35	39	3,100	95	2	385	1	500	12,500	1	1	14·80
31·7	30	122	63	34	—	—	16	9	—	15	4	—	1,000	—	—	9·57
7·8	0	536	—	1	11	3	477	43	1	58	1	500	8,500	1	—	15·71
7·8	30	49	15	15	3	—	7	9	—	16	—	—	1,000	1	—	10·51
14·8	0	9,200†	—	250	1,864	48	6,800	224	14	1,007	—	400	6,600	14	8	14·53
14·8	30	143	49	10	11	2	33	37	1	20	—	30	1,000	—	1	10·35
21·8	0	6,634	—	1	5,840	92	910	147	4	26	3	1,200	4,000	—	1	13·78
21·8	30	403	27	60	65	26	144	81	—	46	—	100	1,000	1	1	12·22
28·8	0	7,992	—	5	283	87	7,600	25	2	107	—	300	9,000	1	2	14·71
28·8	30	655	12	14	62	5	499	62	1	41	2	30	1,000	—	—	12·98
11·9	0§	1,467	13	—	296	30	1,100	25	3	59	—	—	1,000	3	5	15·12
11·9	30§	69	15	2	4	3	24	15	—	8	—	—	200	—	—	10·70

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* In the surface samples from March 13th onwards and in the 30m. samples from April 24th onwards, these were counted under a higher magnification on a fraction of a ruled slide.

† Calculated from partial counts on ruled slides.

§ Sample preserved in 5% formalin.

TABLE V.

	Male Calanus.				Female Calanus.				Stage V Calanus.					Females ‖ Spermatophores and condition of ovaries.				Chemical composition of hauls.		
Date.	Weight of 100 in mg.	Median length in mm.	Protein %	Fat %	Weight of 100 in mg.	Median length in mm.	Protein %	Fat %	Weight of 100 in mg.	Median length in mm.	Protein %	Fat %	% carrying spermatophores.	Early %	Medium %	Mature %	Spent %	Calculated dry weight per haul in mg.	Calculated fat per haul in mg.	Calculated protein per haul in mg.
17.1.33	20·8	2·44	—	20	15·2	2·42	35	27	15·6	2·14	33	27	8·6					9·7	2·6	3·5
			—	28	15·7	2·48	—	—		2·10	39	—								
23.1.33	20·3	2·40	—	—	17·3	2·49	—	—	15·9	2·17	—	—	5·5					8·5	2·2	3·1
30.1.33	16·7	2·29	40	25	12·3	2·32	43	—	11·6	2·04	29	27	13·3					3·8	1·0	1·1
	16·5	2·34	—	—						2·04	—	22								
6.2.33	17·9	2·36	—	27	13·3	2·34	52	24	12·3	2·09	—	34	1·3					6·5	1·7	2·9
					12·6	2·36		22												
13.2.33*	13·6	2·33	—	—	12·8	2·34	—	24	13·1	2·11	—	—	3·3					3·3	0·9	2·4
20.2.33†	13·8	2·34	—	—	15·6	2·32	40	19	16·7	2·25	—	—	0					1·5	0·3	0·6
							—	20												
27.2.33	—	—	—	—	—	—	—	—	—	—	—	—	0					0·3	0·0	0·1
7.3.33‡	12·8	2·33	—	—	13·8	2·29	72	22	13·8	2·12	—	—	0					1·1	0·2	0·7
					13·1	2·31	—	23												
13.3.33	—	—	—	—	—	—	—	—	—	—	—	—	0					0·2	0·0	0·1
20.3.33§	—	—	—	—	15·6	2·32	60	17	14·3	2·15	—	—	0					0·3	0·0	0·2
27.3.33	14·2	2·27	—	—	15·2	2·35	69	21	12·0	2·13	—	30	0					0·6	0·1	0·2
							—	22												
4.4.33	18·4	2·36	—	29	16·8	2·55	55	20	16·5	2·22	31	32	13·0	11	41	36	0	7·1	2·3	2·5
					15·3	2·53	—	—	15·0	2·25	35	31								
10.4.33	22·7	2·45	50	36	22·8	2·67	39	22	23·6	2·36	31	32	15·6	4	37	57	1	17·0	5·3	5·8
	20·8	2·46	42	34	23·6	2·67	39	22	22·4	2·34	33	30								
17.4.33	25·9	2·48	—	31	27·1	2·73	47	26	29·9	2·41	28	33	18·2	0	42	55	3	106·0	35·5	36·8
	26·5	2·50	—	31	26·9	2·73	43	—	28·0	2·40	38	36								
24.4.33	29·0	2·56	33	33	27·7	2·75	36	27	37·5	2·45	37	39	9·9	11	47	42	0	545·8	185·2	192·7
	27·9	2·57	—	32	28·0	2·76	45	30	36·1	2·44	33	31								
1.5.33	23·0	2·53	42	28	24·2	2·72	—	24	22·8	2·38	45	26	2·0	5	29	66	0	250·3	64·5	100·9
	23·1	2·54	—	27	26·7	2·71	—	27	23·7	2·39	35	25								
8.5.33	29·1	2·56	28	30	23·3	2·65	61	24	30·1	2·41	33	37	4·2	3	40	52	3	188·6	64·5	67·2
									28·6	2·43	—	—								
	29·4	2·55	31	—	23·7	2·66	—	25	30·9	2·44	31	36								
									30·0	2·45	—	—								

15.5.33	26·9	2·55	42	26	20·8	2·64	62	20	35·1	2·48	44	27	14·3	10	35	54	1	135·5	35·2	57·9
		2·55	42	25	23·1	2·68	58	20	36·6	2·46	38	26								
22.5.33	26·2	2·52	42	24	19·6	2·59	65	19	27·7	2·36	37	30	12·1	0	12	88	0	109·7	30·4	45·3
	25·9	2·51	—	28	19·9	2·56	—	20	26·4	2·37	—	—								
29.5.33	28·7	2·58	31	28	23·8	2·61	52	19	35·0	2·44	48	26	20·2	1	17	82	0	75·7	21·3	34·7
	29·5	2·58	—	25	23·8	2·57	61	20	33·8	2·41	45	35								
5.6.33	30·6	2·61	31	32	24·8	2·59	52	24	35·0	2·44	32	33	17·1	4	16	79	1	41·9	13·4	14·1
	29·3	2·60	34	32	25·2	2·62	58	20	34·1	2·43	—	33								
12.6.33	32·7	2·60	36	30	26·3	2·59	62	30	35·3	2·42	33	36	1·8	6	8	82	3	42·8	16·1	15·7
	33·4	2·62	—	40	25·6	2·60	—	29	35·0	2·39	36	42								
19.6.33	32·3	2·61	33	—	25·3	2·59	54	20	34·2	2·40	37	31	3·1	5	9	84	2	32·9	9·9	13·6
					23·5	2·56	56	18	35·3	2·39	45	31								
26.6.33	29·6	2·53	42	26	21·1	2·53	61	30	33·9	2·39	34	39	13·6	10	25	64	0	73·9	25·8	28·2
		2·51	35	35	20·3	2·50	—	26	33·2	2·35	36	34								
3.7.33	31·5	2·55	35	30	20·7	2·50	60	26	32·7	2·39	37	40	17·4	44	21	31	2	454·9	167·0	171·9
	30·3	2·53	34	31	20·8	2·50	54	29	34·8	2·38	34	38								
10.7.33	27·6	2·53	42	35	22·5	2·43	62	23	34·2	2·40	38	35	6·6	6	11	82	0	220·9	71·0	92·4
	26·2	2·49	40	35	22·2	2·46	—	23	32·8	2·38	31	36								
17.7.33	23·1	2·38	—	38	18·6	2·40	50	26	29·2	2·30	38	40	4·5	16	23	57	2	159·8	57·1	67·2
					17·5	2·37	—	24	30·5	2·33	43	37								
24.7.33	21·6	2·37	51	27	16·1	2·38	67	18	32·1	2·37	46	36	8·0	14	24	62	0	211·9	68·9	95·5
	21·6	2·36	—	32	17·2	2·43	76	21	31·3	2·34	38	33								
31.7.33	22·2	2·41	41	30	19·1	2·42	61	19	29·8	2·38	37	42	1·5	1	9	90	0	215·3	81·7	88·7
					17·8	2·46	65	20		2·37	—	42								
7.8.33	22·8	2·41	52	31	15·5	2·36	81	20	30·0	2·37	46	39	4·1	10	13	72	3	112·1	41·2	53·5
	23·7	2·43	54	31	15·2	2·40	64	20	29·7	2·35	45	38								
14.8.33	21·9	2·40	41	30	16·4	2·39	73	23	27·7	2·32	32	35	3·2	12	3	79	5	90·4	30·2	31·3
	22·9	2·41	43	32	15·9	2·37	78	22	26·9	2·33	36	32								
21.8.33	19·8	2·37	47	29	14·5	2·28	—	19	27·8	2·34	44	36	8·5	13	8	73	5	86·8	32·0	37·5
	19·4	2·36	50	28	16·5	2·36	—	18	26·9	2·32	41	39								
28.8.33	18·5	2·30	49	30	13·5	2·26	70	25	23·6	2·26	35	36	0	13	16	65	6	71·9	27·5	27·7
					13·5	2·26	67	23		2·23	41	38								
11.9.33	16·3	2·30	—	—	13·4	2·29	65	26	24·4	2·36	37	38	1·8	—	—	—	—	109·9	41·4	40·3
					13·0	2·32	—	—	25·7	2·35	35	39								
2.10.33	—	—	—	—	—	—	—	—	21·6	2·19	—	—	8·3	—	—	—	—	118·2	44·3	43·9
									23·0	2·23	—	—								

* Weight determined on 23 V.

† Weight determined on 42♂ and 21 V. } In all other cases more than 50 were used and usually 100.

‡ Weight determined on 25♂ and 26 V. }

§ Weight determined on 21 V.

‖ Abnormal Calanus are not included in the table.

Notes on the Swimming Methods and Habits of Certain Crustacean Larvæ.

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With 7 Figures in the Text.

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INTRODUCTION.

UNTIL recently most work on larval Decapoda and Euphausiacea had been concerned with the elucidation of the life-histories of various species; latterly, since our knowledge of some of the commoner species has become more complete, other work has been undertaken. For example, Russell and others have clearly demonstrated the existence of diurnal migrations which these larvæ make in the sea, and we now know the extent of the migrations of various species. Other workers have experimented in the laboratory to find the cause or causes of the migrations. Little attention, however, seems to have been paid to the methods by which the migrations are accomplished; such remarks as have been made on the swimming powers and habits of these larvæ are to be found in works mainly devoted to other aspects of the problem. An attempt has been made to bring together some of these remarks and to supplement them with fresh observations on some of the more easily obtainable larvæ.

It must be made clear from the outset that plankton problems are not the only ones connected with the swimming habits of crustacean larvæ. The young crustacean being a free-living larva well adapted to its environment it follows that as swimming is the most important function at this stage of the life-history many of the morphological peculiarities of the larvæ are correlated with it. It has, therefore, been thought advisable to inquire into the closeness of the relationship between the swimming habits and the larval structure. Such a consideration appears to throw a certain amount of light on the functional significance of the abrupt changes of form met with during the life-histories of certain species.

It must be admitted that these two problems, one entirely physiological, the other bearing on points of Morphology and Phylogeny, are not necessarily closely related; but as the observations here recorded appear to merit discussion from both points of view it is convenient to bring these somewhat dissimilar subjects together rather than to deal with them separately.

I have to record my best thanks to the director of the Marine Station, Millport, for the facilities placed at my disposal during my visits to the station and for the regular supplies of plankton received at Glasgow. Also to Dr. W. T. Calman, F.R.S., and Professor J. Graham Kerr, F.R.S., for their advice and encouragement.

Materials and Methods.

The larvæ were observed both at the Marine Station at Millport and in the laboratory at Glasgow. It was found possible to transport larvæ to Glasgow; their normal swimming activities did not appear to be upset by the laboratory conditions. Temperature seemed to be the most important environmental factor, and its careful control was necessary; it was found that the condition of larvæ which had been adversely affected by a rise in temperature during the journey from Millport often improved remarkably after some hours in a more normal thermal environment.

After various methods had been tried it was found that the best way of maintaining an even temperature was to allow a constant stream of cold tap water to flow over the outside of the vessel containing the larvæ. The various jars and tubes in which the larvæ were observed were kept cooled in the same way.

The larvæ were watched in a variety of ways, the currents caused by the actions of the appendages being traced out with suspensions of carmine and indian ink. An attempt was made to test the efficiency of the swimming methods and for this purpose a jar 60 cm. in height by 5 cm. square was used. This jar had a centimetre scale attached to one side and the larvæ were timed by means of a stop-watch when making an excursion of 10 cm. In every case the larvæ were allowed to start moving before the excursion was timed, and so they were given a " flying start."

In order to have some control over the movements of the larvæ the experiments were carried out in a darkened room and advantage was taken of the fact that the larvæ showed definite responses to the stimulus of light. The jar could be illuminated either from the top or from the bottom. It was anticipated that difficulties would arise with convection currents in the experimental jar, but they were found to be negligible. During the experiments no special precautions were taken to control the temperature. The dark-room was unheated and below ground level; its temperature varied little. The glass which was put between the light and the experimental jar was thick, and readings taken at the beginning and end of each experimental period showed that the heat generated by the light did not cause any appreciable rise in the temperature of the water in the jar.

During the experiments on orientation it was found necessary to study the behaviour of the larvæ in darkness. It was found that red light, such as is used for photographic purposes, has no apparent effect on the larvæ. They neither orientate nor swim in response to its presence. These experiments were carried out at Millport and the larvæ were observed by placing the vessel containing them in front of a window of ruby glass in the wall of the dark-room. This window gave light from an adjacent room so that control of the intensity of light falling on it was easy. In all cases the least intensity in which the orientation of the larvæ could be seen was used.

THE SWIMMING METHODS OF THE LARVÆ.

In recording the swimming methods of the larvæ it is convenient to treat of one species in some detail and then to compare and contrast others with it. The type selected is the first larva of *Munida bamffica*, which was abundant in the plankton at Millport in the early spring.

Munida bamffica, first larva.

The larvæ of this species normally progress telson foremost. Motion is brought about by the action of the thoracic exopodites, which cause a stream of water to flow along the sides of the body, over the outside of the carapace and away past the head (Fig. 1). Reversal in the direction of movement was occasionally seen to be brought about by reversal in the direction of the effective beat of the thoracic exopodites, but this was never long continued. The more normal method of reversal, such as is brought into use when the larva collides with some object, is to bring the abdomen and telson slowly under the thorax; the body is then straightened again with a violent jerk, the result being that the animal is sent rapidly head forwards.

In addition to the current caused by the thoracic appendages there is also the respiratory current created by the second maxillæ. This latter current enters the branchial cavities from behind and, passing over the bases of the thoracic limbs, leaves the cavities behind the eyes; the eyes deflect the current outwards (Fig. 1).

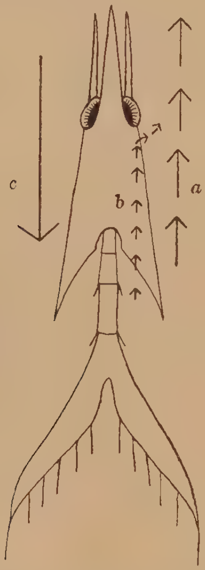

Fig. 1.—*Munida bamffica* (first larva). Diagram to show currents in water. Arrows represent: (*a*) current created by the thoracic exopodites, (*b*) respiratory current, (*c*) direction of movement.

In vertical movements swimming takes place either up or down according to the stimuli which excite the animal to make the excursion. Under experimental conditions it was found that at temperatures between 14° C. and 20° C. movement was towards the source of light. The change of direction of motion when the direction of the source of light was changed appeared almost instantaneous.

When they are not actively swimming the larvæ rest in a horizontal position, and the tendency to sink appears to be very slight. Figure 2 shows the positions of the larvæ during movement and at rest.

A study of the larva of Munida shows that (1) when swimming the body is orientated so that as little resistance as possible is offered to the water: this may be referred to as a "Stream-line effect"; (2) when resting the body is orientated so that the maximum resistance is offered to sinking; (3) that besides the normal swimming mechanism there is a well developed reversal mechanism.

Caridea.

Larvæ of Caridea were not plentiful in the material at my disposal, but two important types were observed, namely, *Pandalus* sp. and *Crangon* sp. The Pandalid larva swam towards the light telson foremost; it swam and reversed in the same manner as a Munida larva. The backward swimming habit has also been noted in the Caridea by du Cane (1839) and by Lyon (1906), who observed it in *Palæmonetes varians;* Lyon also suggested the manner in which the reversal mechanism would be found to work, but said that in this species the action was too quick to be followed by the eye.

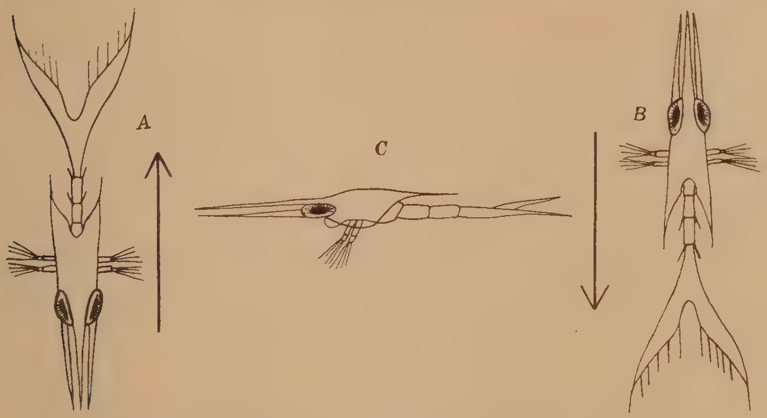

FIG. 2.—*Munida bamffica* (first larva). Diagrams to show orientation when swimming: (*A*) upwards, (*B*) downwards, (*C*) when resting.

The Crangonid larva swam head first. This is important as it shows that the habit of swimming telson foremost is not universal in the Caridea; the significance of this will be discussed later.

Williamson (1901) has also noted that the larvæ of *Crangon vulgaris* progress head first; he also records a spiral movement as do du Cane (1839) and Weldon (1889).

Astacura.

Several larvæ of *Nephrops norvegicus* were observed. In response to the stimulus of light they were found to orientate themselves with the telson and abdomen towards the light, but with the head and thorax in a plane at right angles to them, in the attitude shown in Figure 3. In this posture all the specimens moved towards the light telson first.

The swimming of the larvæ of *Homarus vulgaris* has been described by Williamson (1904), who says that they swim with the abdomen downcurved, as in Figure 4A. They swim forwards. Occasionally he saw the abdomen curved under the body, Figure 4B.

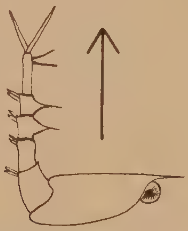

FIG. 3.—*Nephrops norvegicus* (larva). Diagram to show attitude when swimming; movement is in direction indicated by arrows.

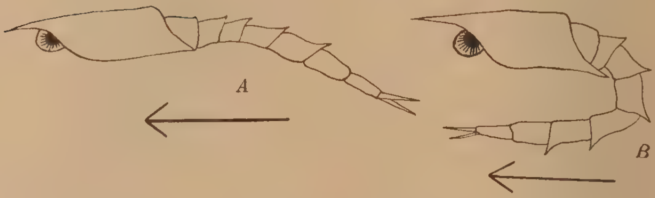

FIG. 4.—*Homarus vulgaris* (larva). Two attitudes seen when swimming. Movement takes place in the direction indicated by arrow.

Anomura.

In addition to the larvæ of *Munida bamffica*, larvæ of the following species were also observed: *Galathea strigosa* (first larva), *G. dispersa* (first larva), *Eupagurus* sp. (last larva), and *Porcellana* sp.

The swimming methods of the majority of these larvæ are essentially the same as those of Munida, but the case of Porcellana is somewhat different.

In Porcellana the larvæ normally progress head first. The long rostrum, however, tends to make them rather unwieldy creatures, and when the direction of stimulus is reversed the direction of the beat of the thoracic exopodites is reversed and the larvæ proceed backwards; they do not rapidly re-orientate themselves as do the larvæ of other Anomurous types; that this is due to the presence of the long rostrum can be shown by cutting it off. When this is done the larvæ swim in the normal manner, but if the direction of the source of light is now reversed the larvæ rapidly re-orientate themselves to it.

The method of reversal in this species is the flexure of the abdomen and telson under the body; they are drawn sharply under the thorax and the larvæ jump backwards.

Spooner (1933) has also observed the swimming habits of certain Galatheid and Porcellana larvæ, and my observations appear on the whole to tally with his account.

The swimming of Anomurous larvæ has also been observed by Thompson (1903) who recorded the backward mode of progression.

Thalassinidea.

Jaxea sp.

A few specimens of this interesting larva were observed at Millport in September, 1933. In swimming they were found to be very like the Anomurous larvæ in habit, but unlike them they were very poor swimmers. However, they orientated themselves with the head away from the light and proceeded towards it telson foremost. The peculiar form of the body, which when flexed is divided into two almost equal portions, each of which presents a similar amount of surface to the water, results in the flexure and extension of the abdomen having no pronounced effect, and the writhing movements which take place move the larva very little, but tend to displace it slightly in the direction of the telson.

Brachyura.

Zoea larvæ of several species of Brachyura were observed; they responded positively to the stimulus of light. The positions adopted when swimming, both up and down, are shown in Figure 5; in both cases the larva is seen to be orientated so that it proceeds dorsal spine foremost. The swimming actions of the thoracic exopodites were occasionally seen to be supplemented by downward jerks of the telson region, but this was rare.

In contrast with the Anomurous larvæ the Brachyurous zoeas sink rapidly when the swimming movements cease, and a larva which appears to be swimming upwards may merely be lessening its tendency to sink. This is due to there being no position of rest; these larvæ remain with the dorsal spine directed upwards, and unless the movements of the thoracic exopodites are continued the larvæ sink.

There is no really well-defined method of reversal, but in the event of a collision the telson and abdomen are violently agitated until the larva is clear of all obstruction.

The swimmimg habits of the Brachyurous zoea were studied by Weldon (1889), who came to the conclusion that the spines were of use to the larva in guiding its movements ; the validity of this assumption will be discussed later.

Although the observations recorded above relate to one stage of the life-history only, namely that in which the thoracic appendages are natatory, they will be sufficient to indicate the nature of some of the problems introduced by the study of the larvæ.

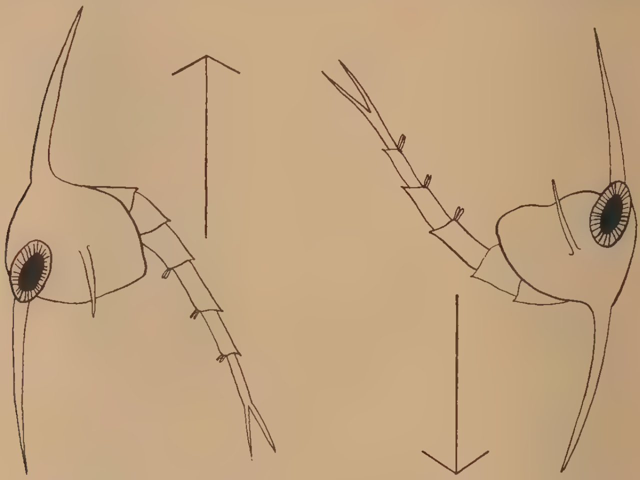

Fig. 5.—Diagram to illustrate the attitude of a Brachyurous zoea when swimming. Movement takes place in the direction indicated by arrows.

These problems may be conveniently divided into two groups :—

(1) The relation of the larva to its environment.

(2) The relation of the larva to other stages of the life-history.

The former presents physiological problems and the latter questions of morphology and phylogeny.

The Relation of the Larva to its Environment.

All larvæ have a tendency to sink. This tendency varies in (1) different species, (2) the same individual. As an example of the first it was found that at 19° C. a larva of *Porcellana* sp. when narcotised sank at the rate of 1 metre in 350 secs., while a Brachyurous zoea of the *Portunus* type, under the same conditions, sank at the rate of 1 metre in 85 secs. In the same individual the tendency to sink will vary with several physical factors, for example viscosity. It will vary also with the orientation of the larvæ to gravity.

Munida bamffica larvæ give a very good example of variation in orientation with respect to movement. Figure 2 shows that when the larva is moving the minimum resistance is offered to the water, whereas while " resting " the maximum is offered. The case of the Brachyurous larvæ is entirely different. All the specimens studied were of the type found in Portunus, that is to say that all four spines of the carapace are present and fully developed. Here there is no position of rest as in Munida, but to prevent sinking the swimming movements have to be continuous. The figure given above (1 m. in 85 secs.) for the sinking of a Brachyurous zoea is for a narcotised larva which sinks in the attitude shown in Figure 6. This attitude is never seen under normal conditions, where the dorsal spine is always directly upwards.

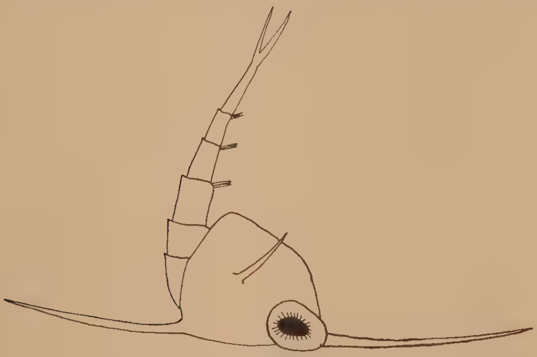

Fig. 6.—The attitude in which a narcotised Brachyurous zoea is found to sink.

This question of orientation is best discussed under the two headings of orientation to (1) Light, (2) Gravity.

(1) *Orientation to Light.*

In the case of orientation to light we are concerned with larvæ in motion. Clarke (1932), working on Daphnia, came to the conclusion that here orientation is a phenomenon with a physiological basis different from that of the other phototactic responses. In the case of Palæmonetes, Lyon (1906) remarked that the larvæ as regards the mode of orientation are negatively phototropic, while in their movements they are positively phototropic ; an idea which also indicates two distinct physiological processes. Spooner (1933) has shown that Decapod larvæ approach the source of light and not necessarily the point of greatest intensity of illumination.

This evidence suggests that certain areas of the eyes function as receptors which detect the direction of light, as appears to be the case in certain insects described by Mast (1924) and others.

Clarke (1930) pointed out that in Daphnia different responses were evoked by small and by large changes in the intensity of illumination; these latter may be considered as shock stimuli. In the observations recorded in this paper shock stimuli were used, and in this case response to the direction of light is all important, the larvæ showing no response to gravity at all; they make excursions in any direction with any side directed downwards as recorded by Weldon (1889), Thompson (1903), and by Spooner (1933).

(2) *Orientation to Gravity.*

The fact that the stimulus of light completely overcomes that of gravity does not show that the latter does not exist, as Thompson appears to imply. When the stimulus of light is removed the larvæ cease to execute forced movements and are free to carry out random movements; it is then that response to gravity is found.

Special attention has been paid to this aspect of orientation in Brachyurous zoea larvæ. In dull red light these larvæ appear to behave as if there were no light present at all. In these conditions they remain with the dorsal spine directed upwards and they carry out random movements in this attitude. The question arises as to how in the absence of light orientation is maintained. Gurney (1902) has pointed out that in the zoea stage there is no organ of balance and he suggested that the spines were in some way connected with this function. Experiments were undertaken with a view to investigating this.

It is clear from narcotising the larvæ that orientation is not a mechanical function of the body, but that it is dependent on consciousness. Amputation of the thoracic exopodites in a conscious larva also results in uncontrolled sinking, showing that orientation is also dependent on the muscular activity of these appendages.

Other functions of the spines which have been suggested are: (1) Protection; (2) Control of the direction of swimming; (3) Adaptation for resisting the tendency to sink.

These functions are not mutually exclusive, but one is probably primary, the others being secondary.

If these suggestions are examined more closely the following evidence is found.

(1) *Protection.*

Gurney (1902) found that small fish such as Gobies had difficulty in swallowing Brachyurous zoeas on account of the spines; and I have to thank Mr. D. P. Wilson, of Plymouth, for informing me in a personal communication that he has seen Pipe-fish when feeding on a catch of mixed plankton deliberately pick out the copepods and avoid Brachyurous larvæ. When feeding the pipe-fish carefully scrutinise one organism after another and no attempt is made to get the zoeas into the mouth. While the cases are of great interest, it is difficult to suppose that small fish which exercise a choice are the chief enemies of zoeas; for in the autumn plankton hauls many Medusæ and Ctenophores were present, and many were found to contain Decapod larvæ. Also Williamson (1904) has recorded that the larvæ of *Homarus vulgaris* eat Cancer larvæ. It would not appear, therefore, that the chief function of the spines is protective.

(2) *Direction of Swimming.*

Weldon (1889) pointed out that the spines of many Crustacean larvæ show a great tendency to develop in one straight line, parallel to the axis of the body; he cites as examples the larvæ of Penæus and Hippolyte and the Galatheidea in general. And he said that the same result is arrived at in a slightly different way in the Brachyurous zoea. Perhaps it is not necessary to point out that this long axis of the body is in most cases the direction of movement. Weldon considered that the possession of these spines enabled the larvæ to make excursions more rapidly and in a more direct manner than larvæ which do not possess such spines. This must lead us to suppose that the spines have been developed to assist swimming movements in a definite direction. On the other hand, it must not be forgotten that if the spines were developed in connexion with some other function they would still control the direction of motion as movement in a plane at right-angles to that of the spines would be impossible for mechanical reasons.

I have to thank Dr. R. Gurney for pointing out that presumably Weldon is here referring to Claus's *Hippolyte* which has since been shewn to be *Callianassa.*

With regard to excursions in direct lines, experiments have shown that if the spines are cut off the larvæ lose none of their powers of swimming in a straight line nor are their swimming abilities in any way upset. It seems more probable that these larvæ owe their powers of direct and rapid movement to the very highly developed swimming mechanism which they possess, assisted, as Gurney's hypothesis would appear to indicate, by an efficient sensory organ functioning as does an otocyst and so helping the larva to maintain a definite orientation.

(3) *Adaptations for resisting the tendency to sink.*

In larvæ such as those of Munida, where a position of rest is taken up, there can be little doubt that the spines help to maintain the animal in a constant position in the water, but in the Brachyurous zoea no such position is known. That is to say, that the large dorsal and rostral spines are never in such a position as to aid flotation. In the case of the narcotised larva, however, these spines immediately come into the horizontal plane; here their effectiveness as adaptations against sinking is shown by the following examples:

(1) Zoea 1.
Temp. 17·4° C.
Normal zoea.
Average sinking time for 6 journeys of 10 cm. . . . . . . 83·4 sec. per 1 m.
Same zoea.
Dorsal spine cut off. Average sinking time for 6 journeys of 10 cm. . . . 66·0 sec. per 1 m.
Same zoea.
Rostral spine also cut off. Average sinking time for 6 journeys of 10 cm. . . 64·4 sec. per 1 m.

(2) Zoea 2.
Temp. 19° C.
Normal zoea.
Average sinking time for 6 journeys of 10 cm. . . . . . . 130·6 sec. per 1 m.
Same zoea.
Dorsal and rostral spines cut off. Average sinking time for 6 journeys of 10 cm, . 121 sec. per 1 m.

There is, however, one period when this position seen in the narcotised larva is taken up during life, and that is during the periods of the moults when the larva has no control over its actions. Any adaptations which would lessen the tendency to sink while the moult is taking place would be an advantage, for the next stage larva would then have a lesser distance to swim up in order to regain its normal position in the plankton.

It may be pointed out that in the Megalopa stage the spines, if present, are small, and during its moult the larva must sink rapidly, so that the young crab stage automatically takes up its position at a greater depth. This point is of interest as Dr. Lebour (1928a) has pointed out that at least in British species there is only one megalopa stage.

(4) *Organs of Orientation.*

The suggestion made by Gurney (1902) that the spines in some way help the larva to orientate never appears to have had much attention devoted to it. Experiments and observations were made on living larvæ with a view to seeing if any facts could be brought to light which would strengthen or confirm Gurney's hypothesis. For the purpose of these experiments larvæ taken in the plankton were used; they were referred to the genera Portunus and Cancer. In the experiments which involved amputation of spines various control methods were devised, and it was shown that the phenomena observed were due to the injuries to the spines and not to the antennæ.

Observations on living larvæ which are not making excursions show definitely that orientation to gravity exists. The behaviour of a normal larva in dull red light has already been described; if the spines of such a larva are cut off either under an anæsthetic or not the behaviour, while remaining normal in the presence of white light, in the red light immediately becomes remarkably different. All sense of direction is lost; a larva that ceases to swim sinks in an uncontrolled manner, and larvæ which continue to swim pursue a spiral course and eventually finish with a spiral dive to the bottom of the containing vessel; once they have reached the bottom they find it very difficult to leave it again. In short, a larva which has had the spines cut off, although it behaves normally in light, in darkness cannot find its way about. The observations recorded above show that Gurney's suggestion is worthy of consideration.

How such an orientation mechanism would work is not easy to see at first glance, but the spines may probably be of assistance in magnifying differential pressure on the sides of the body. It may be noted that the spines appear to be very sensitive to touch, and if any of the four spines are touched with a needle or held with a pair of forceps, the telson is immediately bent round and scrapes the spine as if trying to remove the foreign object, in the same way that Gurney has described it cleaning the dorsal spine (1902).

In this connexion Dr. Lebour (1928b) has pointed out that the larvæ of *Ebalia tuberosa* have only rudimentary spines on the carapace and has suggested that this, together with the peculiar form of the telson, the fork of which is nearly obliterated, may be correlated with their bottom-living habit. Dr. Lebour goes on to point out that the larvæ of *Pinnotheres pisum*, another bottom-living species, show somewhat the same characters, but that the closely related *P. veterum* has all the spines of the carapace normally developed and has also a much larger telson in keeping with the fact that it is not restricted to the lower layers of the water, but is found right up to the surface.

In the absence of further evidence it is impossible to say whether the restriction of these species to the lower layers is due to their tendency to sink having no mechanical check, or whether it is due to these animals failing to find their way about during the hours of darkness.

SPEED OF SWIMMING.

Little appears to be known of the swimming capabilities of Crustacean larvæ; Steuer (1910) records that a small Decapod larva could maintain its position against a current of water moving at the rate of 1 metre in 40 sec. The following are some average figures for specimens timed in the manner described above:—

Galathea strigosa (first larva).	Up at the rate of 1 m. in 50 secs.
,, ,, ,, ,,	Down ,, ,, 45 ,,
Galathea dispersa (first larva).	Up at the rate of 1 m. in 56 secs.
,, ,, ,, ,,	Down ,, ,, 50 ,,
Eupagurus sp. (last larva).	Up at the rate of 1 m. in 50 secs
,, ,, ,, ,,	Down ,, ,, 60 ,,

The above results were obtained at a temperature of 16° C. approx.

Pandalus sp. (late larva) at 17° C.	Up at the rate of 1 m. in 67 secs.
,, ,, ,, ,,	Down ,, ,, 48 ,,
Porcellana sp. at 17° C.	
When moving head first.	Up at the rate of 1 m. in 65 secs.
	Down ,, ,, 55 ,,
When moving telson first.	Up at the rate of 1 m. in 92 secs.
	Down ,, ,, 78 ,,

There are one or two remarks to be made about these figures. Firstly, they do not pretend to be very precise, but are included here as they show a rather remarkable similarity in different species and also approach the figure quoted above from Steuer. Secondly, the effect of gravity in the downward movement is not very noticeable in the smaller larvæ, such as the Anomurous forms, but in some of the larger species has a noticeable effect, for example in Pandalus. Thirdly, it will be seen that the speed of swimming in Porcellana larvæ depends on orientation.

In any attempt to apply these figures to conditions in the sea two uninvestigated factors have to be borne in mind: (1) Fatigue, we do not know how long the larvæ can keep up the speeds found in the experiments. (2) We do not know if the excursions made in the sea are really vertical and as direct as those made in response to an artificial stimulus.

If, however, the experimental conditions are in any way comparable to those found in nature, a migration of 40 metres could be carried out by a Porcellana larva, for instance, in about 40 minutes. This is well within the time given by Russell (1928), who has recorded such a migration taking place within two hours.

From the observations recorded above it is clear that the swimming activities of the larvæ are sufficient to account for the migrations which actually take place in the sea, and there is no need to invoke the aid of physical factors as do the theories of Ostwald and others. As regards the downward movement, it has been suggested that this is not due to the activities of the larvæ, but due to the injurious effect of the light inhibiting their movements so that they sink into deeper water where in the more congenial surroundings they become normally active once again. In my opinion the following facts: (1) that given a suitable stimulus the larvæ swim downwards; (2) that if the larvæ lose their power of movement they become orientated so as to afford increased resistance to the tendency to sink: show that as far as Decapod larvæ are concerned the downward movement is not a passive one, but an active one. Were the inhibition hypothesis correct, one would expect that the process of natural selection would have acted so that on loss of power of orientation the sinking to lower layers of water would have been as rapid as possible.

Finally, a practical point arises: should the vertical migrations in the sea take place at a rate in any way comparable with that found in the laboratory, the validity of conclusions as to the composition of populations as ascertained by horizontal hauls taken over any considerable length of time is brought into question. The experimental evidence leads me to suppose that marked changes in distribution may take place in such a short time as 15 minutes. This may serve to emphasise, if emphasis be needed, the importance of the time factor which has been fully discussed by Russell (1928).

THE RELATION OF THE LARVA TO THE OTHER STAGES OF THE LIFE-HISTORY.

Under this heading several points of morphological interest will be discussed. The larva may be looked upon as a free-living young stage well adapted to its mode of life; it comes between the stage passed through in the egg and the adult. During the larval stages swimming is one of the most important functions and it is not unnatural to assume that many of the structural modifications seen are connected with it. In the next few paragraphs an attempt will be made to indicate how the mode of swimming is influenced by the degree of development reached on hatching from the egg, and how, in turn, the mode of swimming influences the transition of the larva into the adult.

The nauplius is best regarded as a precociously developed head

(Graham Kerr, 1921) and it may be assumed that in an ideal larva the remaining segments of the body would develop in succession, each bearing a pair of appendages. The appendages of the nauplius do not, however, develop in their final form, but are temporarily modified to serve both swimming and feeding functions. When the later appendages appear they take over these duties, allowing the naupliar appendages to be remodelled and to assume the functions which they serve in the adult. In this way the swimming function would be passed backwards firstly to the thoracic and finally to the abdominal appendages.

It is interesting to note that this condition is nearest approached in the Penæidea where the swimming function is passed from head to thorax and then in turn to the abdomen ; but even here a modification, typical of the Eucarida, is to be noted ; this is that the segments of the hinder part of the body develop long before the appendages, and that the posterior thoracic region is compressed ; this leads on to the condition seen in other groups of the Eucarida, for example, the Caridea, where the segments of the posterior thoracic region are not differentiated until the greater part of the abdomen is developed. From the observations recorded above it would appear very likely that these modifications are due to the early need of the reversal mechanism which all these larvæ possess ; also it is for the same reason that the uropods, which form a part of the mechanism, are precociously developed in many species.

The Euphausid type of development is often quoted as being primitive, owing to the very large number of stages passed through ; but the very late appearance of the thoracic appendages would appear to point to a modification of the condition found in the Penæidea, the naupliar mode of progression being retained to a very late stage.

It should be noted that the various accounts of Euphausid larvæ are not very conclusive as to the swimming methods of these animals. From the evidence of Lebour (1925, p. 811) it would seem that the antennæ are the swimming organs until the end of the Furcilia stages is reached. It is during the Cyrtopia stages that the antennæ become differentiated into their adult constituents, and as Dr. Lebour goes on to say that the Cyrtopia merges imperceptibly into the adult one gathers that during these stages the pleopods are carrying out the function which they serve in the adult, namely, swimming. Cannon and Manton (1927), on the other hand, state (p. 247) : ". . . many larval forms, such as Euphausid larvæ, can walk on the endopodites of their thoracic limbs while the exopodites are swimming organs." They do not indicate at what stage the larvæ are observed to swim with the thoracic exopodites ; from Dr. Lebour's careful account it would not appear that this can be seen before the end of the Furcilia stages. Dr. Lebour, as is noted above, also says that the change from Cyrtopia to adult is imperceptible, so it is unlikely that any great change of function takes place here, and, as I have already said, the account given by Dr. Lebour leads me to suppose that during the Cyrtopia stages the appendages are carrying out the same functions which they serve in the adult. The functions of the appendages of the adult Euphausid have been described by Manton (1928), who says (p. 107 *et seq.*) that the pleopods are swimming organs, the thoracic exopodites being mainly concerned in producing a respiratory current. In my own limited observations all the Euphausid larvæ which I saw swam with the antennæ until the pleopods were developed.

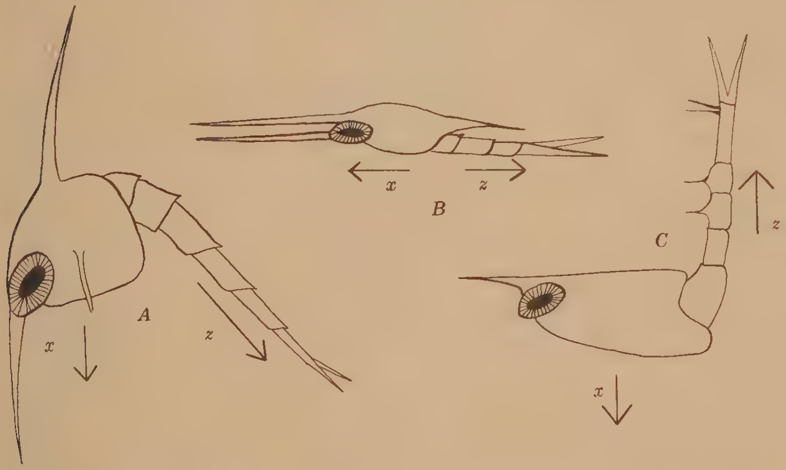

FIG. 7.—(*A*) Brachyurous zoea, (*B*) *Munida bamffica* (first larva), (*C*) *Nephrops norvegicus* larva (not to same scale). Diagram to show the direction of the effective beat of the thoracic exopodites, indicated by arrow *x*, and the direction in which the pleopods would beat if they were functional, indicated by arrow *z*.

In the Caridea although the development of the appendages is delayed, their order of appearance is from front to back, the thoracic exopodites becoming functional in sequence, except that of the fifth pereiopod which is never used for swimming. The Caridea have no naupliar stages so that no direction of movement is imposed upon the mysis stage as it would be if the antennæ were natatory as in the Penæidea. It is this absence of control which has probably resulted in the backward movement found in so many members of this and other groups. In the absence of any foreordained direction of movement the larvæ have been free to move in any direction and it is logical to assume that the backward one has been favoured, as with motion taking place in this direction the respiratory current would assist the movement and not hinder it. Not all larvæ, however, have adopted this method of progression; Crangon is an example of this: here the rotatory movement which has been recorded is probably not due to the absence of spines, as Weldon (1889) supposed, but to a relatively slow rate of movement, as compared with Portunus and Munida larvæ, caused by the antagonistic effect of the respiratory current.

The backward movement has undoubtedly contributed largely to the functional discontinuity between the mysis stage and that stage in which the pleopods first become functional. This discontinuity may also be due, in a large degree, to the postures taken up by different larvæ in which the abdomen is held in such an attitude that any action on the part of the pleopods would result in movement in a different direction to that caused by the action of the thoracic exopodites (see Figure 7).

The difference in the direction of the effective beat of the thoracic and abdominal appendages has been a dominating feature of the evolution of the larval forms of the Decapoda. As a result the natatory function has been confined to the more anterior thoracic exopodites which in such types as the Brachyurous zoea are highly specialised for this purpose.

It is disappointing that there are no records available of the swimming habits of the later larvæ of the Penæidea.* In such a species as *Penæopsis stebbingi*, the development of which has been described by Gurney (1927), it is difficult to imagine any abrupt change in swimming habits between the naupliar and mysis stages, the development of the thoracic appendages being very gradual; there is, however, a rather abrupt change to the Mastigopus stage. A form in which this latter change appears to be less marked is that of Acetes recorded by Brooks (1882). The functional significance of this discontinuity in the Penæidea is at present unknown, but occurring in this series of larvæ it is interesting as there is no apparent reason why the change from mysis to mastigopus should not be as gradual as that from nauplius to mysis. The explanation may lie in a difference of posture of thorax and abdomen such as has been described in other larvæ.

SUMMARY.

The swimming methods and habits of certain Decapod larvæ have been observed. The first larva of *Munida bamffica* was chosen for special attention. Such a study shows the importance of (1) orientation, (2) the presence of a reversal mechanism.

Observations on other types show these factors to be of great import-

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* Gurney (Ann. Mag. Nat. Hist. Ser. 9, Vol. 18, 1926, p. 26) has dealt with the swimming methods of Penæid larvæ in general terms but apart from Müller's observations there quoted we have no records of the attitudes in which these larvæ swim, especially in response to external stimuli.

ance and also show that there are a great variety of attitudes in which larvæ swim.

Points in the relation of the larvæ to their environment were next considered; orientation is again important here, but whereas in Munida larvæ a "resting" orientation is found no such attitude is seen in Brachyurous zoeas.

Orientation to light was found to overpower completely orientation to gravity, but orientation to gravity exists, and it is argued that Gurney's hypothesis, which connects the spines of the carapace with the maintenance of equilibrium, should be examined more closely.

It is suggested that in the Brachyurous zoea the spines are of use as adaptations for lessening the tendency to sink mainly during the periods of moulting.

The speed of swimming has been considered and it is found that at temperatures of 14° C.–18° C. Anomurous larvæ can travel at the rate of 1 metre in 1 minute. This is a time well in accordance with Russell's results, obtained in the English Channel. Here fatigue is an unknown factor and it is not known if the whole migration is carried out in one stage; if it were a migration of 40 metres such as Russell records it might take place in 40 minutes.

Reasons are given for believing that the downward migration of larvæ found at dawn is due to the activities of the animals themselves and not to physical factors or to passive sinking due to inhibition of movement resulting from an injurious effect of light.

The origin of some of the structural adaptations of the larvæ is discussed. The precocious development of the posterior region of the body is considered to be due to the early need for a reversal mechanism, provided for by the caudal fan at the end of a flexible abdomen. The importance of posture when swimming is pointed out and it is maintained that the backward movement seen in so many larvæ has helped to emphasise the metamorphosis between the last mysis stage and that in which the pleopods first become functional.

The backward movement itself is considered to be due to the absence of a naupliar stage in the life-history; thus the mysis has no foreordained direction of movement and so in many cases swims backwards in order that the respiratory current will aid rather than hinder the speed of movement.

The swimming habits of crustacean larvæ and their bodily form are thus seen to be closely related.

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The Biology of *Balanus balanoides.* I. Growth rate and its relation to Size, Season and Tidal Level.

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With 4 Figures in the Text.

THREE workers have contributed recently to our knowledge of the growth rate of *Balanus balanoides* : Runnström (1925), and Hatton and Fischer-Piette (1932). The former kept a single patch of barnacles under observation for a year at Herdla, which is about 27 km. north-west of Bergen. By estimating at different times of year the size distribution of the spat, and of the first and second year groups, which he could differentiate by their size, colour and shape, he obtained a curve for the growth of the animal for the normal duration of its life. His investigations also cover the maturation of the gonads. And he finds that the normal course of life is for the animals to settle on the rocks in April. Towards the end of the following year the ovaries are developed, and in the spring of the third year the larvæ are liberated. Most of the adults die after this, only a possible few surviving to spawn the following spring. His measurements comprise the length only of the shells, and he says that the successive year groups may be distinguished by their degree of flattening.

Hatton and Fischer-Piette (1932) worked on the growth of individuals near St. Malo during the greater part of two years, and investigated the effects of varying degrees of shelter and tidal level on this growth rate. Their results will be referred to in greater detail later in this paper, but they may be summarised in the following two relations : the most larvæ settle, and the greatest growth takes place, at the most exposed places, and at the lowest tidal levels. They show also that growth is at a maximum from April to June-July, and practically at a standstill for the rest of the year.

METHODS.

In the present work it was felt that it would be desirable to employ a method of measurement which would allow of the calculation of the volume of the animal. This is necessary in the first place to cope with the variations of shape as between individuals, and in the second place to afford a measure which, unlike length, increases more or less in a simple ratio with age. Such a measure is more than ever necessary when, as Runnström states, the animal is continuously changing its conicity throughout life (although no such change has been detected at Port Erin). In the present paper, where the volume of the animal is referred to, this is the volume of a cone with a height equal to the height of the apex of the shell above the surface of attachment, and a basal diameter equal to the average of the length and breadth of the base. Such an assumption takes no account of the truncation of the cone, but it gives a value related sufficiently closely for our purposes to the external volume of the animal, and it is the only such value which may readily be obtained from measurements of the animal taken *in situ* on the rocks. It is hoped in a future paper, to relate this calculated volume to the true body weight of the barnacle. Where the length of the animal is given, this is the length of the base through the rostrum and carina, as in the two works referred to above.

The locality chosen was a vertical face of rock, facing south-west, in a long cleft in the rocks running from low to high-water in the Dub Reef in Port Erin Bay. The position is fairly exposed, with few fucoids growing on the rocks. Three patches of barnacles were selected on this surface, one near the bottom of the barnacles zone (B. 1), one higher up (B. 2), and a third (B. 3) at the extreme top of their range. By inspection these patches seemed quite typical for this region. Their levels, at the mid-height of the patches, are as follows :†

B. 1. —0·75 feet O.D. or about mid-tide level.
B. 2. +2·74 feet O.D.
B. 3. +4·58 feet O.D., or about high water of neap tides.

Full scale photographs allowed of the identification of individuals, about a hundred of which were kept under observation on each patch for a whole year. At intervals of from one to two months each individual was measured (length, breadth and height), and as soon as the new spat were large enough for measurements in the field, a series of these also was included. A note was made also of all individuals which died, and whose shells were either empty or missing.

As the newly settled spat were too small for measurement *in situ*, a number of these were distinguished by a ring marked round them on the rock, and a series of them was brought in from time to time for accurate measurement in the laboratory. When the barnacles are small, it is possible to detach them from the rocks without damage. Two sets of these small barnacles were collected, the first group " O " representing typical animals which had settled about the end of April, while the second group "Q" represent spat which settled later in the year, and whose growth was apparently retarded at first by the summer heat. Finally the length of about eight hundred barnacles in each of the groups B. 1, B. 2 and B. 3 was measured in June 1932, and from these a size-distribution diagram was obtained for each group for the date in question.

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† Levels determined by Mr. J. R. Bruce. The tidal range at Port Erin is about ± 4 feet for average neap tides, and ± 8 feet for average spring tides.

TREATMENT OF RESULTS.

The individual measurements for each patch, about five thousand in all, are too numerous to reproduce here, but their analysis is given in Tables I, II and III. For each patch of barnacles there is a series of readings from which the volumes can be calculated as described above, for each of about a hundred individuals, and taken at five to seven times in the year. Each of these periods has been dealt with separately, and in it the individuals have been grouped according to their size at the commencement of the period, the limits of each group having been so chosen as to include an adequate sample. The limits of experimental error in the initial measurements are of the order of about ±10%. This is reduced in the grouping together of a number of animals, but since the groups vary in size, no final error can be given which would be universally applicable. In each of the groups, as shown in the tables, the stated volumes and volume increments are the means of all the individuals comprised in the group. From the increase in volume in each group the *growth rate* has been calculated, this being defined as the average percentage increase in volume per ten days.

RELATION OF GROWTH RATE TO SIZE.

The figures show very marked differences in the growth rates of the barnacles, both at different sizes and at different times of the year, as well as at different levels. Comparison of the last two factors is rendered difficult by the very much greater growth rates of the smaller individuals. In Figure 1 (and Table IV), seasonal variation has been eliminated, by plotting the year's mean growth rate against size and shows the difference of growth rate with size, as well as the fact that the barnacles are growing faster at successively higher levels.

SEASONAL VARIATION IN GROWTH RATE.

The seasonal variation in growth rate may be seen from the figures in the last columns of Tables I, II and III by interpolating values to allow of the comparison of animals of the same size. The simplest condition, found in the smaller animals of all the patches, is that of an animal having a high growth rate for a short period in the spring or summer, followed by a period of slower growth throughout the winter. The time of maximum growth rate varies on the different patches, and with different sizes of barnacles, but sufficient information is not yet available to allow of an interpretation of these differences. It is to be hoped that they may become clearer when more is known about the seasonal changes in the soft parts of the barnacle. In the larger individuals of B. 1 and B. 3, there is, in addition to the summer growth period, a second period of increased growth rate in the winter, which in the largest members of B. 3 considerably surpasses the summer rate. The fact that such a winter period is not shown in B. 2 may possibly be due to the overwide spacing of the winter readings.

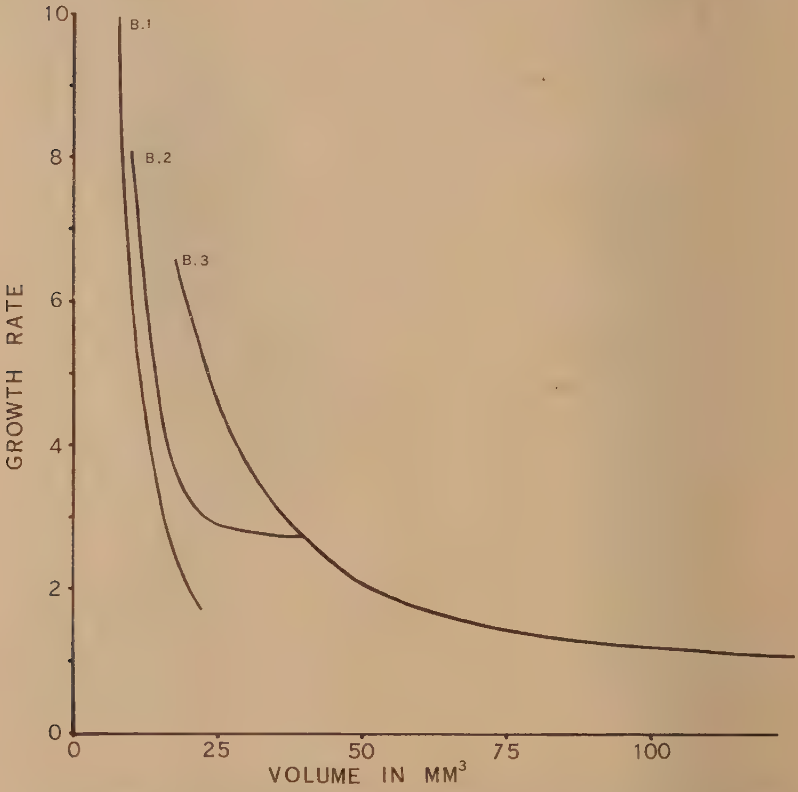

Fig. 1.—Relation of mean yearly growth rate to size. The rate is greatest in the smallest individuals, and in those at the highest level (B. 3).

The Growth of the Newly-settled Spat.

All the data discussed up to this point, concern barnacles which were sufficiently large to be measured *in situ* on the rocks. It is necessary to consider here the growth curves obtained for the spat of the " O " and " Q " groups, samples of which were periodically brought into the laboratory for measurement. The measurements of these are given in Table V, and the results are shown graphically in Figure 2.

On April 25th, 1931, large numbers of Cypris larvæ commenced to settle on the rocks, and a first sample of metamorphosed individuals was collected on April 30th. The individuals marked at this time comprise the " O " group, and represent the typical members of the community. Later in the year a number of very small individuals were noticed, whose size suggested that they were newly settled. On October 5th these had a volume of 1·75 cu. mm. as compared with an average volume for the " O " group of 12 cu. mm. A number of these small individuals were ringed, and they comprise the " Q " group. The suggestion that these were newly settled spat was however disproved by a photograph of the rock surface taken on July 22nd in which some of the " Q " group were seen to be already present. It would appear, therefore, that these " Q " barnacles settled later than the " O " ones, and were not able to get through their early period of rapid growth before the heat of the summer.

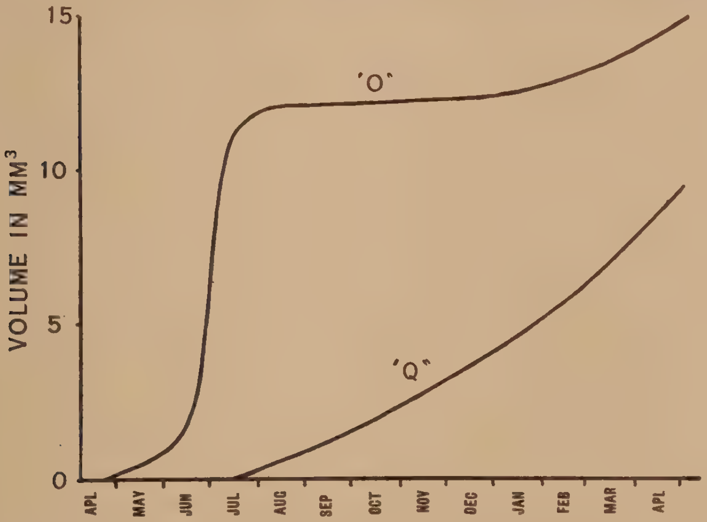

Fig. 2.—Growth of young individuals during their first year. The " O " group are typical, and the " Q " group late-settled specimens.

Figure 2 shows the retarding effect of the summer hot period on the barnacles of both groups. By the beginning of the following year, the "Q" group have made good progress, and are catching up with the "O" group, so that in May their respective volumes are 9·6 and 14·9 cu. mm. One point which emerges from the comparison of these two groups is that the wide differences of size found in first-year barnacles is not maintained in the second year, thus justifying the choosing of a definite size as representing the typical barnacle of any age, as is done below. As the barnacles of the "O" and "Q" groups were not taken from the exact level of any of the three patches, their results have not been utilised in the calculation of the initial portion of the curves shown in Figure 3.

The Growth of a Typical Barnacle through Successive Years.

The measurements have been carried out for one year only, but, since they cover the whole range of sizes of individuals found in the locality, it is possible to construct from them a curve representing the whole life of a barnacle. This assumes that the year of observation was a typical one. The temperature observations in Port Erin Bay throughout the period do not suggest that the year 1931-32 was very abnormal.

The first measurement, *in situ* on the rocks, of the young barnacles was made in August 1931 when the average first-year members of the groups B. 1, B. 2 and B. 3 had volumes of 4·66, 8·84 and 6·38 cu. mm. These figures are based on too small a number of individuals to be accurately representative, but they suggest that the greatest growth of young spat takes place at the middle of the zone (B. 2), and then successively less well at the top of the zone (B. 3) and at the bottom of it (B. 1).

Commencing with the above sizes, and using growth rates for each period, which were read from curves relating growth rate to initial size, the growth of a typical barnacle for each patch was calculated for a series of years. The figures so obtained are given in Tables VI, VII and VIII, and the results are shown graphically in Figure 3. The calculations have been continued in the case of B. 1 and B. 2 into their third year, and in the case of B. 3 into its fourth year. As will be shown later this represents the span of life of the majority of the individuals of B. 1 and B. 2, but a portion only of the life of many individuals of B. 3.

It will be seen from Figure 3 that, with the exception of the first year, the growth rate is greatest on B. 3 and slightly less on B. 2. The deficiency in the first year is regained by B. 3 by the beginning of the second year, and from then on members of B. 3 are always slightly larger than members of B. 2 of the same age. Throughout the whole of its life B. 1 has a much smaller growth rate than either of the other patches.

Runnström's data give a length at the end of the first year (Dec.–Jan.) of about 6·5 mm., and for a similar period in their second year of about 9·5 mm. Hatton and Fischer-Piette's figures for the same ages are between 2·5 and 3·0 mm. for the first year, and about 5·5 mm. for the second year. They do not give sufficient data to allow of the conversion of these data into volumes, but if the Port Erin figures are expressed as length, the results are as follows :—

	HERDLA.	PORT ERIN. B. 1	PORT ERIN. B. 2	PORT ERIN. B. 3	ST. MALO.
Length at the end of the first year	6·5 mm.	4·7	5·3	5·2 mm.	2·5–3·0 mm.
Length at the end of the second year	9·5 mm.	6·5	7·6	8·1 mm.	5·5 mm.

Thus in all cases the values for Port Erin lie between those of Runnström and those of Hatton and Fischer-Piette. The former does not state the level in his locality, or its condition with regard to exposure. In the case of Hatton and Fischer-Piette's figures there is a considerable difference at the end of the first year in the sizes attained in sheltered and in exposed positions; but this difference appears from their graph to have been entirely made up in the second year, although they do not mention the fact in the text.

The sequence of growth rates in these three localities is of interest since it is that of ascending latitude, the growth rate being highest in the most northerly latitudes. (St. Malo 49° N., Port Erin 54° N. and Herdla 60° N.)

LENGTH OF LIFE.

According to Runnström, most of the barnacles die after spawning, in their third year, only a possible few living to spawn again the following year. The data to be considered below show that, while this is true for the lowest zone (B. 1), and to a lesser extent for B. 2, the members of B. 3 may live for five or six years, and probably considerably longer.

It is a general observation on most parts of the coast which are not very exposed, that barnacles are smaller near low water, and become steadily larger towards high water : and further that at the extreme top of their range, there are found individuals much larger than are found anywhere lower down. In order to obtain an expression of these differences, between 700 and 1000 individuals were measured on each of the three patches, in June 1932. Owing to the large number of measurements required, lengths only, and not volumes were taken, but volumes were obtained by formula from the lengths, as will be explained later. It must be emphasised that the object of this set of readings was to obtain a measure of the frequency of occurrence of the larger members of the community, and not to obtain the year group sizes. Thus, owing to the large size of the groups taken, the exact position of the size group peaks is somewhat masked in Figure 4.

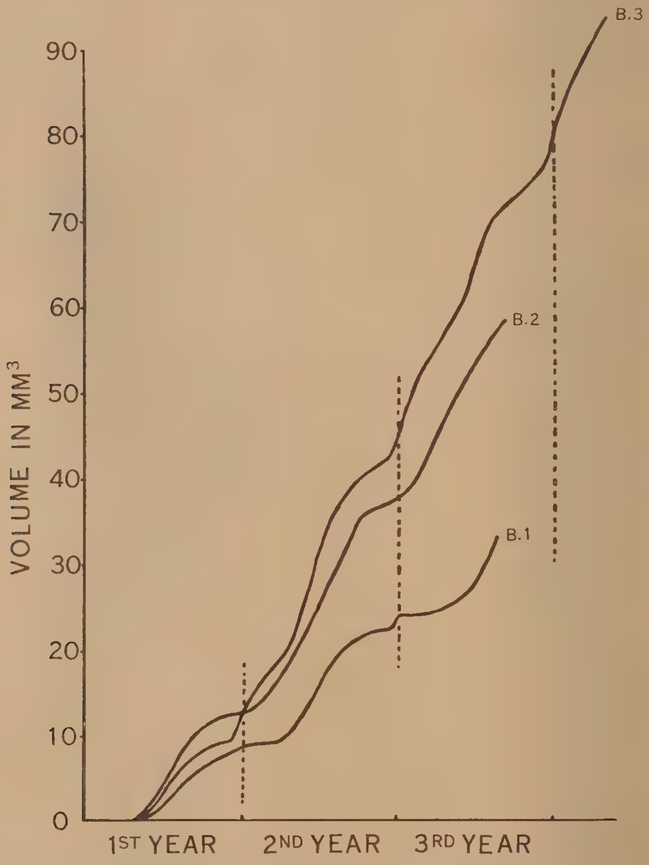

Fig. 3.—Growth throughout the life of typical individuals at the three levels. The curves for B. 1 and B. 2 represent the normal duration of life at those levels, but B. 3 individuals may live for perhaps six or more years.

The lengths were measured, as in Runnström's work, through the rostrum and carina. The percentages in each millimetre group—neglecting the spat—which were too small to be measured accurately—are given in Table IX. The spat were counted, and their numbers are entered in Table IX, but these have not been taken into account in the calculation of the percentages.

In Figure 4 these percentages have been plotted against lengths. It must be remembered, in examining this graph, that while volume is approximately a straight line function of age, length is not so. A curve has therefore been superimposed in Figure 4 relating volume to length for the barnacles in question. This has been drawn from the formula

$$\text{length} = \sqrt[3]{\frac{\text{volume}}{0{\cdot}084}}$$

which has been arrived at by taking the mean value of $\frac{\sqrt[3]{\text{volume}}}{\text{length}}$ for various sizes, in all individuals measured during the year. Runnström stated that there was a change of apical angle of the older barnacles.

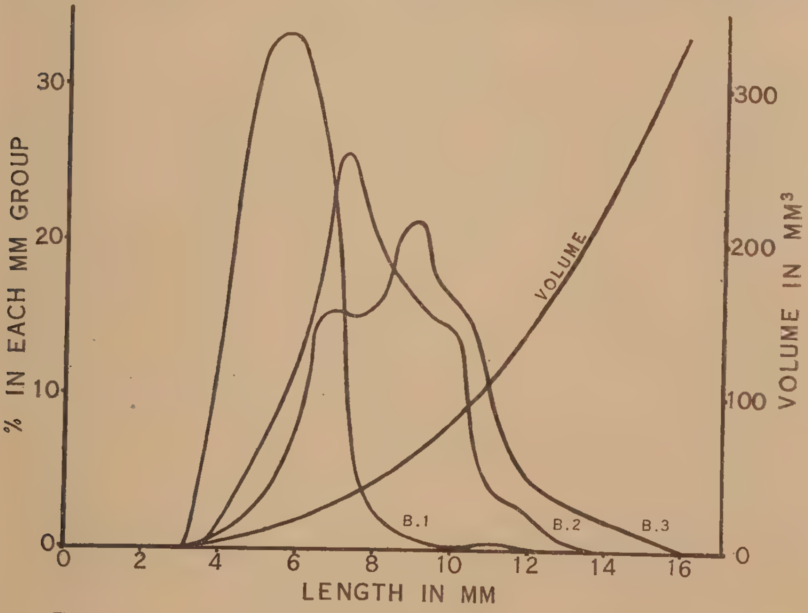

Fig. 4.—Size distribution curves for the three patches, and a curve relating to length volume.

Our groups do not show any trace of such a change, although it has been noted on other parts of the Manx coast, especially where there is much overcrowding ; and also elsewhere in isolated specimens growing under estuarine conditions. Since in our group there is no change of shape, and the volume is a straight line function of the cube of the length, such a formula may legitimately be used to interpret the lengths of Figure 4 as volumes.

Although not produced for this purpose, Figure 4 indicates the sizes of the various year groups on the three levels in June, and these values bear out the validity of those which have been obtained by the other methods already described. B. 1 shows a second year peak only, B. 2 a second and a doubtful fourth year peak only, and B. 3 second and third year peaks. The three curves show clearly the size differences at the three levels, especially if the lengths are translated into volumes from the curve included in the figure for that purpose. Summarising these results we get the following :—

4% of B. 1, 58% of B. 2, 72% of B. 3 have a volume greater than 50 cu. mm.

0·3% of B. 1, 18·5% of B. 2, 33·0% of B. 3 have a volume greater than 100 cu. mm.

0·0% of B. 1, 0·0% of B. 2, 6·0% of B. 3 have a volume greater than 200 cu. mm.

The difference in average age on the three patches is further borne out by the death-rate observed on them in the course of the observations. The number of animals from which these figures are drawn, is small, but their differences are too great to be the result of chance.

Death-rate per 100 individuals per year.

B. 1	B. 2	B. 3
35	21	3

The above figures concern only animals of about four months old and over. The death-rate on B. 3 is surprisingly low, and it may be noted that not one of the deaths in that group occurred among the very large specimens.

It has already been noted that there is a relatively sparse population in the top, B. 3, zone, and also that small individuals are relatively slightly less common at that level. In other words, on the top zone the young barnacles find it hard to gain a foothold, and to attain a sufficient size to withstand the adverse conditions there, but having once attained a sufficient size, they are likely to grow faster and to live longer than they would have done at a lower level where their earlier life would have been easier.

Hatton and Fischer-Piette's work shows clearly the greater numbers of young Balanus settling at lower levels, but the meaning of their mortality figures is less clear. At their most exposed locality the mortality at the end of the first year, is considerably less at low water than higher up the shore. On the other hand, in a more sheltered locality, the mortality for the first year becomes steadily greater towards low water. Unfortunately they give no figures for the mortality on the highest patch of all, at the top limit of the Balanus zone.

General.

The difference of level of the three groups of Balanus studied is not very great. It covers, however, the whole range for the shore at Port Erin. B. 1 was typical of all those barnacles growing at that and a lower level on the beach, that is to say, on this beach, down to about three feet below mean sea level. B. 2 was typical of the intermediate zone, and B. 3 of the small uppermost zone. The latter is the upper limit of their distribution, and although a few may be found slightly higher, none extend more than two feet higher, that is to say above 7·5 feet above mean sea level.

The B. 1 type of barnacles are small, and usually rather less numerous than the B. 2 type. The latter are undoubtedly the most numerous on the shore, and hence may be taken as typical. The B. 3 type, although less numerous than B. 2, is usually much larger. It almost certainly spawns many times in its life, and, being large, produces a large amount of spawn. The B. 2 type, on the other hand, usually spawns only once and then dies. (Runnström, 1925, p. 39.) It is therefore possible that the B. 3 type plays a much more significant part on the shore than its numbers would suggest. It is hoped in a later paper to extend this account to less, and more exposed localities.

I should like to express my indebtedness to Mr. J. R. Bruce for assistance in making some of the measurements, and to all members of the staff here who have assisted at various times; also to Prof. J. H. Orton and Dr. E. J. Allen for helpful criticism of the paper.

SUMMARY.

1. The volumes of *Balanus balanoides*, at three levels of the shore, have been observed for a year.

2. The young barnacles grow very much faster than older ones.

3. The growth rate varies greatly with age, season and tidal level, but in general there is a period of maximum growth in the summer, and very little growth in the winter.

4. Growth, except during the first year, is greatest higher up the shore.

5. Young barnacles, which settle too late in the year, have their growth retarded by the summer heat, but almost catch up in size the earlier settled spat, by the beginning of the next year.

6. The growth rates found are intermediate between those recorded from Herdla (near Bergen), and those from near St. Malo.

7. Most of the lower- and middle-zone barnacles die in their third year, but those from the extreme top zone may live for five years or more.

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TABLE I.

THE GROWTH RATES ON THE B. 1 PATCH THROUGHOUT THE YEAR.

Volumes in cubic millimetres. Growth rate is the percentage increase in volume per ten days.

	Date.	Initial volume range.	Initial volume average.	Final volume average.	Mean volume for the period.	Growth rate.
1931	5 May	0–6	3·98	9·34	6·66	26·9
	to	6–8	7·1	13·0	10·5	16·64
	20 June	8–12	9·25	13·4	11·32	8·96
		12–	17·4	20·1	18·7	3·1
	20 June	0–8	5·4	10·43	7·91	15·0
	to	8–13	10·8	15·6	13·2	7·18
	21 Aug.	13–17	15·1	19·8	17·45	5·02
		17–	20·3	25·5	22·9	4·13
	21 Aug.	0–4	2·86	4·9	3·33	9·8
	to	4–6	5·28	8·24	6·76	7·68
	2 Nov.	6–16	10·9	14·0	12·45	3·89
		16–	21·1	23·6	22·35	1·62
	2 Nov.	0–6	4·47	5·07	4·77	3·83
	to	6–10	8·66	9·05	8·55	1·28
	7 Dec.	10–20	14·2	14·5	14·35	0·61
		20–	25·6	25·9	25·75	0·33
	7 Dec.	0–7	5·27	6·24	5·75	5·12
	to	7–10	8·85	10·13	9·49	4·03
1932	12 Jan.	10–15	12·07	13·29	12·68	2·81
		15–	21·0	22·6	21·8	2·11
	12 Jan.	0–7	4·64	4·94	4·79	1·38
	to	7–15	10·24	10·36	10·30	0·25
	9 March	15–	22·63	22·73	22·68	0·09
	9 March	0–5	3·94	5·84	4·89	8·61
	to	5–7	5·89	7·73	6·81	5·70
	3 May	7–10	8·85	10·50	9·67	4·02
		10–	12·77	14·30	13·53	2·18

TABLE II.

The Growth Rates on the B. 2 Patch throughout the Year.

Volumes in cubic millimetres.

	Date.	Initial volume range.	Initial volume average.	Final volume average.	Mean volume for the period.	Growth rate.
1931	12 Jan.	0–4	3·1	8·3	5·6	15·75
	to	4–8	5·65	12·55	9·1	11·85
	25 April	8–15	10·6	16·8	15·7	5·68
		15–25	19·4	25·4	22·4	3·0
		25–	36·6	44·3	40·35	2·20
	25 April	0–7	5·6	11·9	8·75	20·1
	to	7–10	8·5	14·0	11·25	11·5
	20 June	10–15	11·7	16·1	13·9	6·72
		15–20	17·4	22·5	19·95	5·06
		20–30	24·0	30·6	27·3	4·92
	20 June	0–12	9·6	14·2	12·9	7·75
	to	12–15	13·3	17·8	15·55	5·45
	21 Aug.	15–20	17·6	22·5	20·05	4·26
		20–	31·4	39·4	35·4	4·10
	21 Aug.	0–7	5·1	8·3	6·7	11·2
	to	7–10	8·6	11·3	9·95	5·62
	16 Oct.	10–13	11·4	14·9	13·15	5·49
		13–19	15·9	19·5	17·7	4·5
		19–30	24·4	29·6	27·0	3·81
		30–	38·9	46·2	42·55	3·34
	16 Oct.	0–10	7·12	8·57	7·84	2·27
	to	10–15	12·60	13·87	13·23	1·12
1932	14 Jan.	15–20	17·40	18·50	17·95	0·70
		20–	32·4	33·8	33·1	0·48

TABLE III.

The Growth Rates on the B. 3 Patch throughout the Year.

Volumes in cubic millimetres.

	Date.	Initial volume range.	Initial volume average.	Final volume average.	Mean volume for the period.	Growth rate.
1931	13 Jan. to 29 April	0–6	4·2	8·8	6·5	10·4
		6–10	8·01	13·25	10·7	6·22
		10–30	21·9	32·0	26·95	3·91
		30–40	34·7	47·0	40·85	3·35
		40–70	57·1	68·25	62·6	1·86
		70–	129·0	142·0	135·5	0·95
	29 April to 13 June	0–18	11·3	16·4	13·8	10·0
		18–40	22·3	29·7	26·0	7·4
		35–50	43·1	48·1	45·6	2·6
		45–55	51·0	54·0	52·5	1·74
		55–75	63·2	66·2	64·7	1·41
		75–	124·5	132·5	128·5	1·43
	13 June to 18 Aug.	0–20	15·0	26·2	20·6	11·3
		20–30	23·2	31·9	27·55	5·68
		30–40	34·7	44·1	39·4	4·12
		40–70	53·45	63·32	57·88	2·51
		70–	147·2	154·6	150·9	0·76
	18 Aug. to 19 Oct.	0–5	4·10	5·44	4·7	5·28
		5–15	8·44	10·82	9·63	4·55
		15–30	21·9	24·7	23·3	2·60
		30–45	38·0	41·5	39·75	1·49
		45–55	50·4	52·8	51·6	0·77
		55–65	60·6	63·6	62·1	0·80
		65–80	70·9	73·6	72·75	0·62
		80–	126·0	129·6	127·8	0·46
	19 Oct. to 9 Dec.	0–10	6·15	8·15	7·15	5·35
		3–15	10·35	11·72	11·03	2·27
		10–50	31·8	33·8	32·8	1·0
		50–	97·1	101·5	99·3	0·74
	9 Dec. to	0–10	7·09	10·07	8·58	11·65
		10–30	19·05	22·90	20·97	5·62
1932	14 Jan.	30–50	38·91	43·16	41·03	3·04
		50–70	58·7	63·2	60·95	2·13
		70–	94·1	100·64	97·87	1·93

TABLE IV.

RELATION OF YEAR'S MEAN GROWTH RATE TO SIZE AT THE THREE STATIONS.

Volumes in cu. mm.

B. 1		B. 2		B. 3	
Volume.	Growth rate.	Volume.	Growth rate.	Volume.	Growth rate.
7	9·95	10	8·08	17·5	6·59
10	5·94	12	6·10	20	5·85
13	3·84	15	4·32	25	3·12
16	3·25	17	3·74	35	2·04
19	2·09	20	3·27	50	1·41
22	1·70	30	2·86	75	1·19
		40	2·71	100	1·05
				125	

TABLE V.

VOLUMES (IN CU. MM.) OF YOUNG INDIVIDUALS IN THEIR FIRST YEAR.

"*O*" *Group.*	Date.	Volume.	
1931	April 25	—	Just settling on the rocks.
	April 30	0·103	
	May 14	0·329	
	June 9	1·20	
	July 1	5·57	
	July 29	12·5	
	Aug. 22	11·7	
	Sept. 15	12·6	
	Dec. 7	11·5	
1932	May 7	14·9	

"*Q*" *Group.*	Date.	Volume.	
	July 22	—	Visible in photographs.
	Oct. 5	1·75	
	Dec. 7	3·28	
	May 7	9·60	

TABLE VI.

Calculated Growth throughout the Life of a typical Member of B. 1 Patch, as deduced from Curves drawn from Table I; the initial Volume, on August 21, 1931, being 4·66 cu. mm.

	Period.	Volume at commencement of period.	Growth rate during period.
1st year	Aug. 21–Nov. 2	4·66	8·00
	Nov. 2–Dec. 7	7·38	1·68
	Dec. 7–Jan. 12	7·82	4·18
2nd year	Jan. 12–March 9	9·00	0·30
	March 9–May 1	9·13	3·58
	May 1–June 20	10·93	7·26
	June 20–Aug. 21	14·89	5·10
	Aug. 21–Nov. 2	19·60	1·80
	Nov. 2–Dec. 7	22·17	0·37
	Dec. 7–Jan. 12	22·46	2·06
3rd year	Jan. 12–March 9	24·13	0·08
	March 9–May 1	24·22	0·84
	May 1–June 20	25·34	1·53
	June 20–Aug. 21	27·28	3·99
	Aug. 21–	33·53	

TABLE VII.

Calculated Growth throughout the Life of a typical Member of B. 2 Patch, as deduced from Curves drawn from Table II; the initial Volume, on August 21, 1931, being 8·84 cu. mm.

	Period.	Volume at commencement of period.	Growth rate during period.
1st year	Aug. 21–Oct. 16	8·84	5·74
	Oct. 16–Jan. 12	11·68	1·11
2nd year	Jan. 12–April 25	12·85	4·46
	April 25–June 20	18·75	4·98
	June 20–Aug. 21	23·99	4·10
	Aug. 21–Oct. 16	30·09	3·56
	Oct. 16–Jan. 12	36·09	0·49
3rd year	Jan. 12–April 25	37·68	2·16
	April 25–June 20	46·08	4·92
	June 20	58·73	

TABLE VIII.

Calculated Growth throughout the Life of a typical Member of B. 3 Patch as deduced from Curves drawn from Table III; the initial Volume, on August 18, 1931, being 6·38 cu. mm.

	Period.	Volume at commencement of period.	Growth rate during period.
1st year	Aug. 18–Oct. 19	6·38	5·61
	Oct. 19–Dec. 9	8·59	2·63
	Dec. 9–Jan. 13	9·97	9·20
2nd year	Jan. 13–April 29	13·26	5·60
	April 29–June 13	21·13	6·60
	June 13–Aug. 18	27·40	5·35
	Aug. 18–Oct. 19	37·06	1·38
	Oct. 19–Dec. 9	40·23	0·86
	Dec. 9–Jan. 13	42·34	2·83
3rd year	Jan. 13–April 29	46·64	2·28
	April 29–June 13	57·89	1·57
	June 13–Aug. 18	61·98	2·13
	Aug. 18–Oct. 19	70·68	0·63
	Oct. 19–Dec. 9	73·44	0·76
	Dec. 9–Jan. 13	76·84	1·93
4th year	Jan. 13–April 29	82·18	1·41
	April 29–June 13	94·36	1·42
	June 13	100·40	

TABLE IX.

Size Distribution (Lengths, in mm.) on the three Patches on June 2, 1932. Lengths measured to the nearest whole mm. The 1932 Spat, shown in Brackets in the numbers Column, are excluded in the Calculation of the Percentages.

	B. 1		B. 2		B. 3	
Length.	No.	%	No.	%	No.	%
1	—	—	—	—	—	—
2	(597)	—	(559)	—	(437)	—
3	—	—	—	—	1	0·33
4	44	13·4	4	1·22	3	0·99
5	102	31·1	20	6·14	8	2·64
6	108	32·9	39	11·9	24	7·94
7	64	19·4	81	24·8	47	15·5
8	8	2·43	65	19·8	48	15·8
9	2	0·61	52	15·9	64	21·1
10	—	0·0	45	13·8	49	16·1
11	1	0·33	13	3·98	29	9·60
12	—	0·0	7	2·14	13	4·30
13	—	—	1	0·31	9	2·97
14	—	—	—	—	5	1·65
15	—	—	—	—	3	0·99
16	—	—	—	—	—	—
Total	329 +(597)		327 +(559)		303 +(437)	

A Comparison of the Biology of *Echinus esculentus* in Different Habitats.

Part I.

By

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With 5 Figures in the Text.

The material for this study of racial differences in *Echinus esculentus* was obtained from three grounds in the neighbourhood of Port Erin, Isle of Man. The three grounds differed widely in nature, and hence the means of capture, and the ease of obtaining adequate samples was different for each ground. The first locality, designated " Breakwater," is on the lee side of a ruined breakwater in the mouth of Port Erin Bay, entirely submerged at high tides, but accessible by boat at low water. The Breakwater stands on a bottom of sand and shell, in a depth of about five fathoms. It is composed of loose concrete blocks, largely overgrown with *Balanus balanoides* and *Spirorbis borealis*. It is too exposed to support a very large Fucoid vegetation, but in the lower zones there is a very heavy growth of *Laminaria cloustoni*, *L. digitata*, and *Saccorhiza polyschides* with an undergrowth of *Gigartina stellata*. The urchins were collected with a long-handled net, and thus include some individuals which were actually exposed to the air, and others from a depth down to about one fathom at low water. In this particular locality urchins are extraordinarily abundant, and large numbers are exposed at low water of spring tides.

The second ground, the " Breast," lies about a mile off Port Erin, and in a depth of 17·20 fathoms (Fig. 1). The bottom is sand and shell, with a typical fauna (**4**, p. 36, Pl. I). Urchins were obtained from it with a small otter trawl. The third ground—" Chickens "—lies about four miles west of the Chickens rock in 37 fathoms, on a bottom of rather muddy sand mingled with boulders. The urchins are obtained from this ground in traps set by the fishermen to catch " Buckies " (*Buccinum undatum*). The urchins obtained from these creels are of small size, and it has been suggested that this is due to a selective action in the catching power of the creels. But this is negatived by the fact that similar creels, similarly baited, and set on inshore grounds, in a depth of about five fathoms, habitually take large numbers of large urchins. As only twelve creels were in use, and the supply from them was dependent on visits from fishermen, the number of urchins from this ground was limited, and the data obtained from them are in general not as full as those from the other two grounds. The present paper is concerned more particularly with the first two grounds, and it is proposed to discuss in another paper the special significance of the "Chickens" type of urchins.

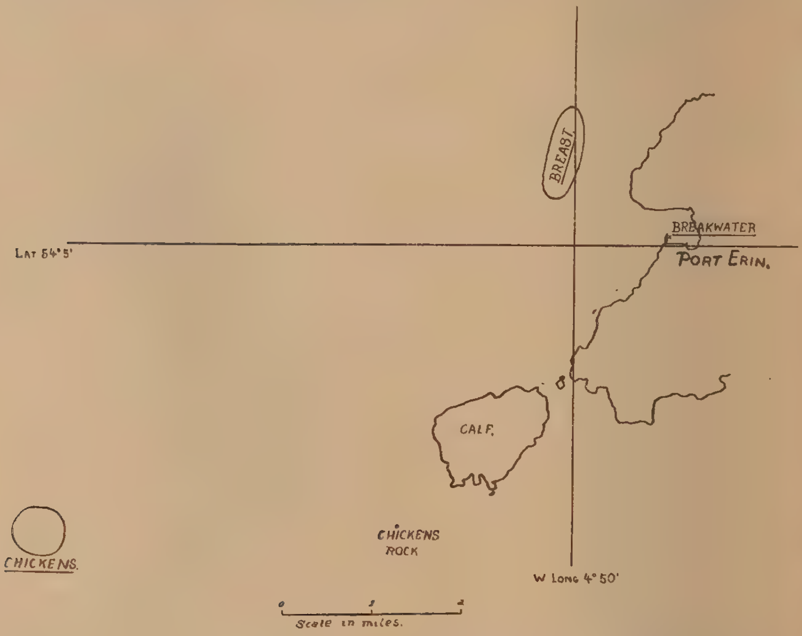

FIG. 1.—Map of the south end of the Isle of Man showing the positions of the grounds from which the three types of urchins were obtained—Breakwater (Littoral), Breast (17–20 fathoms), and Chickens (37 fathoms).

METHODS.

Wherever possible, samples of at least fifty individuals were taken, but as this was not always possible, the numbers used are in every case indicated in the tables. In a few cases, samples taken from the same ground within a few days have been grouped in order to obtain an adequate sample. With regard to the adequacy of the sample, those from the breakwater were always from exactly the same locality, and the samples are fairly regular in their constitution. Those from the Breast and Chickens are, on the other hand, liable, from the method of their collection, to come from slightly varying localities, and the resulting irregularity is apparently reflected in the less regular graphs obtained from these grounds.

The following measurements were taken, though not all of them were obtained from every specimen : *Test diameter*, taken with pointed-ended calipers between the spines. *Test height*, measured in the same way. *Test volume* (TV), obtained by immersion of the whole animal in a vessel full of sea-water, and fitted with an overflow, so that the displacement could be measured. *Gonad volume* (GV), estimated by immersing the whole gonad, after removing it from the animal, in a measuring cylinder containing a known amount of water. A series of measurements of *Shell thickness*, in conjunction with certain other factors, was made on a separate series of specimens from each ground. The measurement was made under a microscope, fitted with a micrometer eyepiece, on the ground edge of the shell, the latter having been cut at mid-height, at the suture of the inter-ambulacral plates. These shell thicknesses will be discussed in more detail in a future paper.

Ripeness was estimated by examination under a microscope of a pipette sample taken from the gonad, and smeared on a slide. The criterion of ripeness varied slightly in the two sexes. Since the male products are mostly ripe by the time they are shed into the cavity of the gonad follicle, the smear would not normally show many spermatogenesis stages, even in an unripe individual, although these would be present in the follicle wall. The presence of a considerable number of ripe and active sperm in the cavity of the follicle has been taken as the criterion of the ripeness of the male, but this does not mean that many more sperm may not be in the process of ripening. In the case of ovaries if unripe ova are present in the follicle at all, these will be found in the smear, along with any ripe ova which are present. In the case of females ripeness was recorded only when more than about 95% of the ova were actually ripe. Although this difference of criterion between the two sexes will in part account for the apparent earlier ripening of the males, it does not seem to do so entirely, and it must be remembered that the males so recorded as ripe were at least capable of yielding considerable quantities of ripe sperm.

Physical Conditions on the Grounds.

A general description of the nature of the grounds has already been given. The sea temperatures for Port Erin Bay, and hence for the Breakwater specimens, are discussed later. The temperatures on the Breast are less extreme than those in the shallow waters of the Bay, and further, the intertidal specimens will, if above low water, be exposed to extremes of air temperature from which those living below low water are protected. Not much is known of other conditions on the grounds beyond the obvious fact that there is much more light on the Breakwater ground than on either of the other two. How this factor may affect the urchins is not known. The Breakwater is very much richer in food than either of the other two grounds, and examination of the urchin gut contents shows that those from the Breakwater are feeding largely on *Balanus* and algæ, both of which are very abundant in this littoral zone. Algæ appear to form a big proportion of the diet, and the specimens from the two deeper water grounds will only be able to obtain an algal diet from such weeds as may drift out to sea and settle on their grounds. The bottom on the Chickens ground is probably rather muddy, and it is known that it is bordered on the seaward side by a region of deeper water and mud bottom on which Echinus could not thrive.

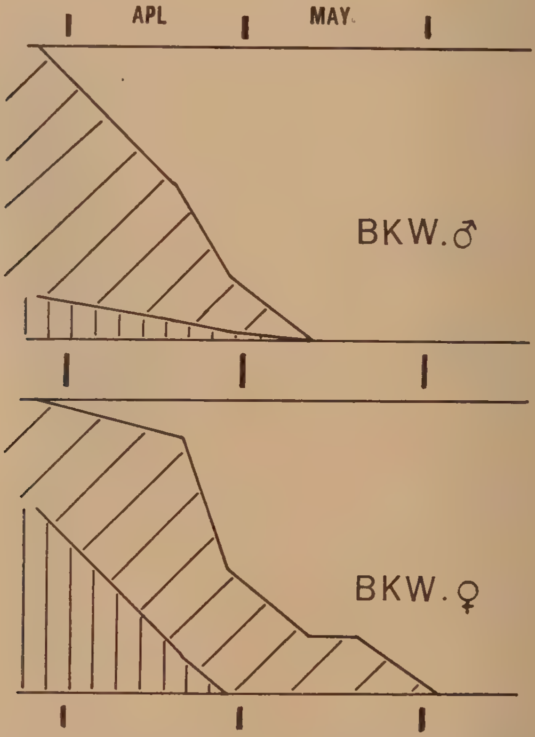

FIG. 2.—Diagram showing the relative proportions (%, vertical scale) of unripe, ripe, and spent urchins of either sex on the Breakwater in 1931. For details see Fig. 3.

Ripening of the Gonads.

The available data on the condition of the gonads throughout the year are given in Tables III, IV, and V, and are also shown in Figures 2 and 3. The 1931 spawning was watched in detail on the Breakwater only, but that of 1932 was watched on all grounds. The gonad condition during the intervening period was watched on the Breakwater and Breast, but sufficient material was not available from the Chickens. It will be seen in the first place (Figs. 2 and 3) that on all grounds the males ripen before the females. The partial explanation of this has been mentioned already. On the Breakwater the males ripen during the summer, and are nearly all ripe by the autumn ; while fully ripe females do not begin to appear until February, and during the early part of the spawning time, spent females may be found alongside unripe individuals. On the Breast the males begin to ripen later, i.e. in October, and are nearly all ripe by the end of February, when the females commence to ripen. The data from the Chickens are few, but the gonad condition on that ground seems to follow a very similar course to that on the Breast.

Gonad Volumes.

In order to allow of the comparison of the sizes of gonads in animals of different ages, the gonad volume has been expressed in Figure 4 and Tables I and II as ten times the actual gonad volume, divided by the test volume $\left(\frac{10.GV}{TV}\right)$. The test volume has been chosen as a measure of size of animal in preference to test diameter, since the relative height may vary considerably both with increasing age, and among individuals of the same age from different grounds. At first the animals were divided into several size groups, and these considered separately, but it was found that there was no difference of relative gonad size according to the size of the animal, so all sizes were eventually grouped together, thus allowing larger samples, and more accurate results. In the same way there was found to be no difference in the time of spawning, according to the size of the individual, so in considering the time of spawning, all sizes have again been grouped together.

The great difference in size attained by the gonads on the Breakwater and on the Breast is most noticeable (Fig. 4), and is specially significant when it is remembered that the gonad is the only organ of the body in which the urchin is able to lay up a reserve of food material, and that the Breakwater affords the richest feeding-ground. That the whole of the food so stored is not required for spawning is indicated by the fact that the gonad volumes on the Breakwater do not ever fall as low as the

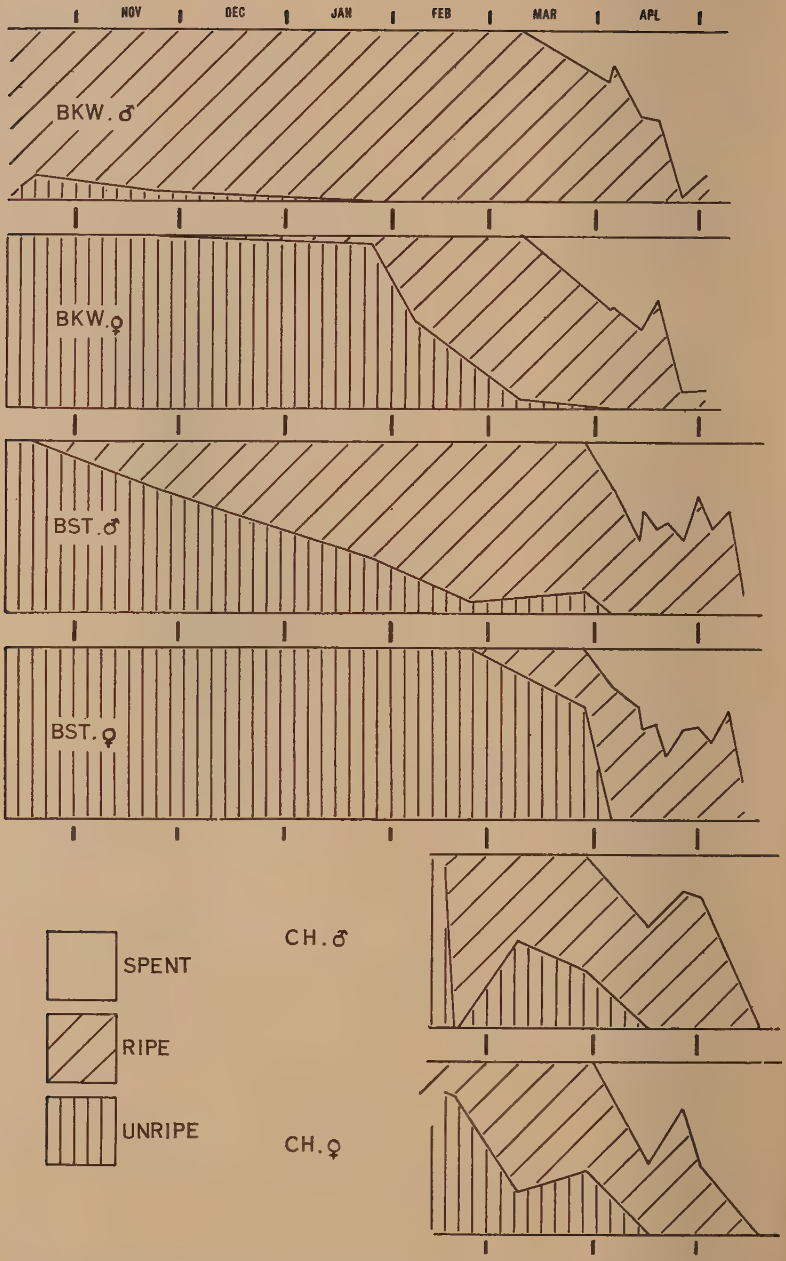

Fig. 3.—Diagram showing the relative proportions (%, vertical scale) of unripe, ripe, and spent urchins of either sex on the three grounds in 1932—Breakwater (BKW), Breast (BST), and Chickens (CH).

maximum value obtained by the gonads in the Breast. This is true not only of the population as a whole, but also of individuals. The Breakwater urchins never become spent completely, while on the Breast the spent

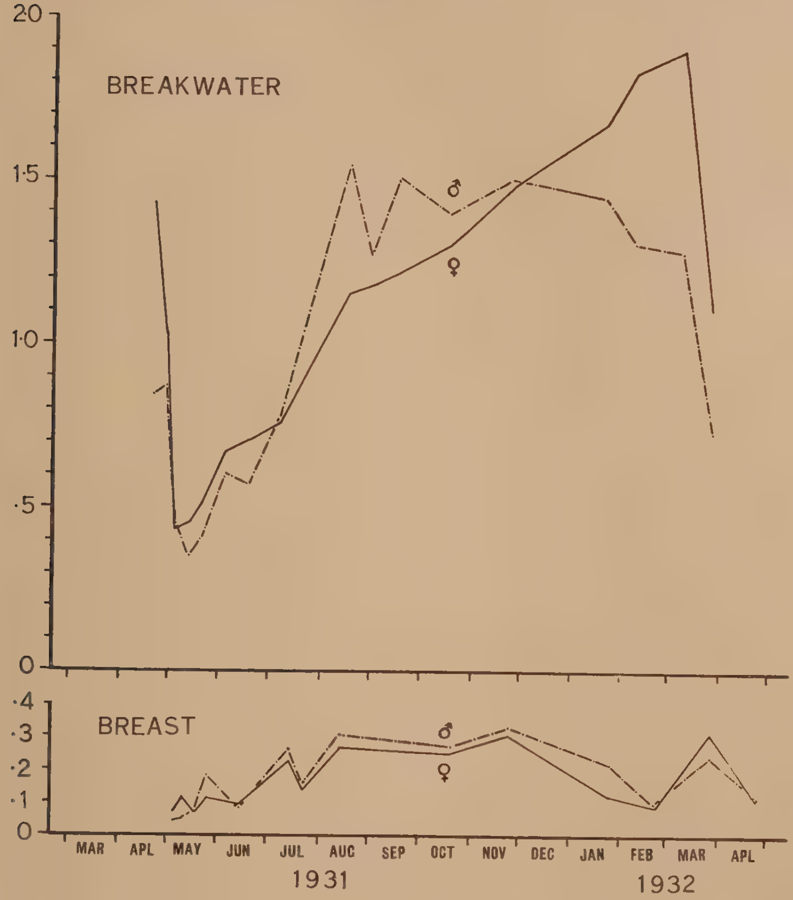

Fig. 4.—The seasonal variation in the volume of the gonads of urchins from the Breakwater and Breast grounds in 1931–32. The gonad volumes are expressed as ten times the actual gonad volume divided by the test volume of the animal.

gonad is reduced to a very small trace. At their maximum the Breast gonads attain a value of $\frac{10.GV}{TV}$ of only ca.0·4 while the values on the Breakwater rise as high as 2·0, and even higher in individuals.

On the Breakwater the males attain their maximum gonad volume in August, and then remain more or less constant until spawning sets in. The females, on the other hand, increase rather more slowly, but their gonads continue to grow in volume right up to the time when spawning commences, and by then they are considerably larger than those of the males. On the Breast both sexes seem to run a more or less similar course, reaching their maximum about August, but the variation between successive samples somewhat masks the finer details of the process. The drop in the gonad volumes in both sexes on this ground in Jan.–Feb. may be due to inequalities of sampling, but may, on the other hand, have a real significance. But since the data are insufficient to decide either way, the point need not be discussed here, although it would be most interesting if it could be investigated further.

Stott (3) has described the changes in the percentage of glycogen, total carbohydrate, and total fats in the gonads of urchins from the Breakwater, during maturation and over the period of spawning. In the first place he finds no significant difference in the percentages of any of these between the two sexes, and as the various percentages vary during the year, they do so more or less similarly in both sexes. The percentage of total fats does not seem to alter much throughout the year, but the percentage of total glycogen in the gonad rises very sharply after spawning (his first post-spawning measurement is in June), and then drops steadily until spawning again occurs. There is a suggestion that this glycogen is being converted into some other form of carbohydrate, at any rate immediately prior to spawning. Now he shows that the percentage of glycogen in both ova and sperm is considerably less than it is in the whole gonad from which they were obtained. This fact, together with the sudden rise in the percentage of glycogen in the gonad when the ripe genital products have been shed, suggests that the food reserves are stored in the form of glycogen in the nutritive bodies in the gonad, and are transformed into other substances as they are absorbed into the ripening genital products. Further, his data with regard to the similarity of carbohydrate and fat percentages in the two sexes, in conjunction with the evidence of different behaviour in the rate of increase of size of gonad in the male and female (Fig. 4), suggests that there must be a marked difference in the feeding behaviour between the male and female, since the former produces fresh gonad very rapidly, and then remains little changed throughout the late summer, autumn, and winter, while the female is continuously increasing throughout this period. Finally the full female has a gonad about twenty per cent bigger than that of a full male.

TIME OF SPAWNING.

The only reliable data for 1931 are for the Breakwater, and these are shown in Figure 2. The results for all grounds for 1931 are shown in Figure 3 and all are tabulated in Tables III, IV, and V. The 1932 spawning, at any rate on the Breakwater, took place between two and four weeks later than it did the preceding year, that is to say it took place in April–May in 1931 and in March–April in 1932. On the Breast and Chickens, spawning took place about a fortnight later in 1932 than on the Breakwater, and on all grounds the spawning period covered about two months. Whereas, however, the spawning of both sexes is more or less complete on both the deep water grounds, on the Breakwater relict sperm and ova are retained in considerable quantities in the gonads, and artificial fertilisations were readily made with them throughout the summer, and even as late as Christmas.

The Relation of Spawning to Temperature.

The later spawning of the Breakwater urchins in 1931 as compared with 1932 is associated with lower temperatures in the water of the bay in the year of later spawning (Fig. 5). The year's minimum temperature occurred in both 1931 and 1932 in the second week of March, and in both years spawning commenced within a few weeks of this date. In 1931 spawning commenced about the end of March, when the temperature in the bay was about 6·5° C., and in 1932 it commenced about the first week of March at a temperature of about 7·2° C. But, since the exact date of the commencement of spawning is difficult to determine accurately, it is preferable to compare the dates at which 50% of the community are spent. This took place in 1931 at a temperature of 7·0° C. and in 1932 at 7·8° C. No temperatures were recorded on the Breast in either of these years, but in 1933 the Breast temperatures at the spawning season were about 0·5° below the corresponding temperatures in Port Erin Bay. This would correspond with a lapse of about a fortnight before the Breast attained the temperature at which spawning set in on the Breakwater. Although this is only a rough approximation, it is in agreement with the lag of about a fortnight between the times of spawning on the Breakwater and Breast. In 1931 (Fig. 2) the urchins of both sexes ripened considerably later on the Breakwater than they did in 1932, and this also is perhaps associated with the lower temperatures in the winter of the former year.

Orton (2) records that urchins taken in from five to ten fathoms at Plymouth, spawned from April to June, when the temperature ranged from about 9·0° to 13·0° C. At Millport, in the Clyde, the spawning period given by Elmhirst (1) is from February to August, with a maximum in May. This corresponds with a temperature range there of about 7° to 13° C. with a maximum spawning at about 9·8° C. Our figures of 7° to 8° are therefore slightly lower than those for Millport, and

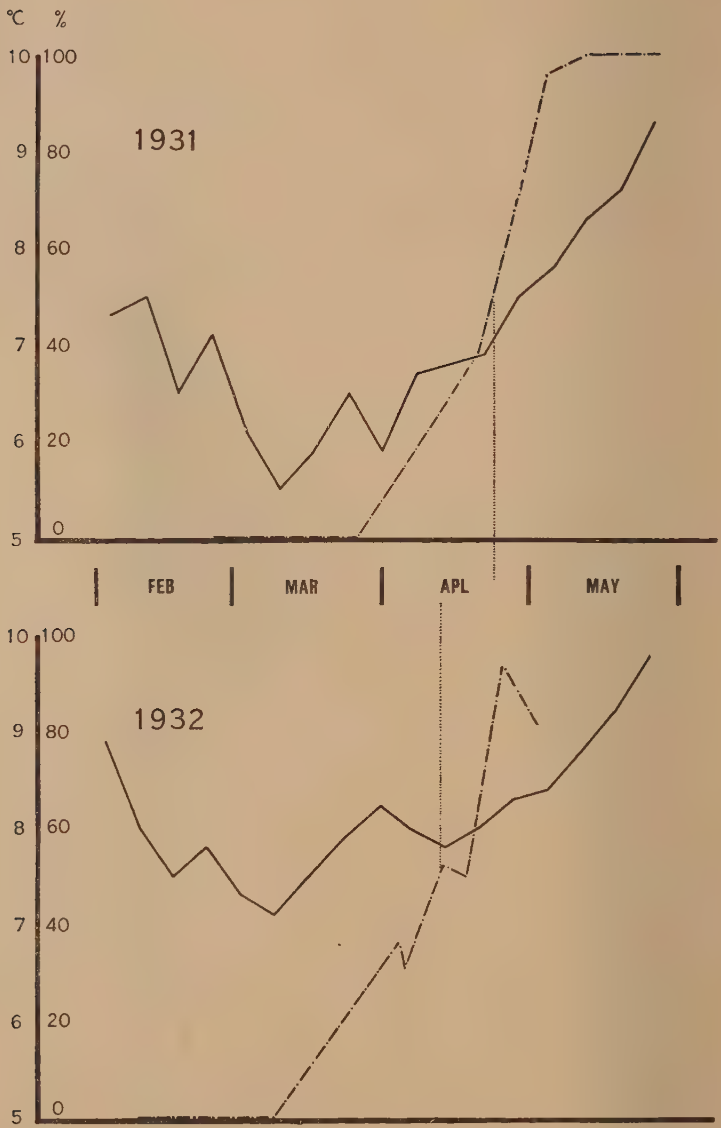

Fig. 5.—The relation of spawning (percentage of spent individuals—broken line) to temperature (whole line) on the Breakwater in 1931 and 1932. The position of 50% spawning is indicated by a vertical dotted line in each case.

definitely lower than those for Plymouth. Also the spawning time seems to be about a month earlier here than it is at either Plymouth or Millport. But in all three localities the commencement seems to follow fairly soon after the temperature first starts to rise, although the interval would seem to be least at Port Erin.

GENERAL CHARACTER OF THE URCHINS FROM THE THREE GROUNDS.

The Breakwater urchins show a greater range of colours than those from deeper water. The Breakwater ones range from violet to rusty red, the colour being present throughout a fairly thick layer in the surface of the test. The Breast and Chickens practically never show a violet colouration except in the spines, the test colour varying between pale brown and reddish.

Shape is not a good criterion since it varies greatly with age ; a young specimen of 1 cm. diameter having a value of $\frac{\text{height}}{\text{diameter}}$ of 0·52 while one of 7 cm. diameter will be considerably taller with a value of about 0·7. But this varies on the different grounds. A small sample taken in about 3½ fathoms at the Niarbyl, north of Port Erin, had a normal H/D value at 1 cm. diameter, but at 4 cm. it was 0·8. Specimens of the same size from the Breakwater were not nearly so tall. In fact these were the tallest specimens found here. There seems, further, to be a tendency for the largest specimens to flatten somewhat. The largest specimen taken by us on the Breakwater had a diameter of 12·1 cm., and an H/D of 0·63.

In shell thickness there is a regular difference between the Breakwater and the Chickens urchins at all sizes, the shell thickness for a Chickens urchin of 4 cm. diameter being 0·71 mm., while that of a Breakwater urchin of the same size is 0·96 mm. The Breast urchins are of a curious type, the young ones having a shell thickness typical of what a young Breakwater one would have were such ever found (see below), while the adults from the Breast have the typical thickness of the rarely found adult Chickens urchin. It is not intended to discuss in the present paper more than the fact that such a well defined difference does exist between the urchins from the three types of ground. Its significance will be dealt with in another paper.

Finally, the three grounds differ markedly in the size of the urchins which are found on them. On the Breakwater no very small specimens are taken, the smallest which I have seen being 2·5 cm. diameter, and even this was in 1933 when exceptionally small specimens were being taken there. Normally, urchins are hardly ever seen there with a diameter of less than about 7 cm. The same may be said of the littoral specimens obtained at the Niarbyl and in the Calf Sound, at the former of which localities urchins are abundant between tide marks on a low spring tide, but in the Sound a few only are taken. On all these grounds it is normally only large specimens which are taken. Specimens up to 10 cm. in diameter are common on the Breakwater. The largest I have seen at Port Erin measured 12·1 cm. in diameter, and came from the Breakwater, but even larger ones have been recorded there.

On the Breast, on the other hand, all the smaller sizes are very abundant, and 8 cm. diameter is about the maximum size usually attained ; a few are taken up to 9 cm., but I have not seen any as large as 10 cm.

On the Chickens ground similarly, all the smaller sizes are abundant, but here the maximum size is even smaller, few over 4 cm. diameter being taken, and none over eight. In this case it is probably a case of the migration of the larger individuals off the ground, but the discussion of this probability is postponed until more data are available.

SUMMARY OF RESULTS FOR THE BREAKWATER AND BREAST.

There are two types of ground at Port Erin, differing widely in the general environmental conditions, and each with a characteristic type of urchin on it. The difference is sufficiently well marked for the local fishermen, who collect the urchins for sale to summer visitors, to distinguish them as different types. The littoral urchins from the Breakwater are larger and thicker shelled than those from the Breast. Their gonads reach a greater maximum size, and, in fact, never fall as low even as the maximum volume for the Breast urchin gonads. This difference is probably correlated with the much greater food supply on the Breakwater, since the gonad is the one organ of the body in which the animal can store reserve food material. Spawning commences in March or April and lasts for about two months, but is slightly earlier on the Breakwater than on the Breast. Ripening also takes place considerably earlier in both sexes on the littoral ground. Spawning seems to set in at a temperature of about 7° C., and the colder winter of 1931, compared with 1932, was associated with a later ripening and spawning in the former year. Similarly it is suggested that the slightly later spawning on the Breast than on the Breakwater is correlated with the slightly later rise in the temperature of the water on the deeper water ground in the spring.

I wish to express my indebtedness to Prof. J. H. Orton who is responsible for the inception of this work on Echinus, as well as for the examination of a number of the earlier samples: I am also indebted to Miss E. C. Herdman for obtaining some of the trawled material for me, and to Mr. J. R. Bruce for examining certain samples in my absence.

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TABLE I.

SEASONAL VARIATION IN THE GONAD VOLUME ON THE BREAKWATER.

	♂		♀	
Date.	$\frac{10\,GV^*}{TV}$	Number of specimens.	$\frac{10\,GV}{TV}$	Number of specimens
1931				
April 21	(0·84)	27	(1·43)	10
April 29	(0·87)	33	(1·03)	19
May 5	0·45	19	0·43	6
May 13	0·35	13	0·46	32
May 21	0·41	4	0·51	10
June 4	0·61	18	0·67	29
June 19	0·57	18	0·71	34
July 7	0·78	16	0·76	43
August 18	1·54	5	1·16	23
September 1 . . .	1·27	3	1·18	9
September 17 . . .	1·51	2	1·22	7
October 18	1·39	26	1·30	30
November 25 . . .	1·50	18	1·48	18
1932				
January 26 . . .	1·44	31	1·67	19
February 8 . . .	1·31	29	1·83	18
March 9	1·28	27	1·90	21
March 28	0·73	12	1·11	13

TABLE II.

SEASONAL VARIATION IN GONAD VOLUME ON THE BREAST.

	♂		♀	
Date.	$\frac{10\,GV^*}{TV}$	Number of specimens.	$\frac{10\,GV}{TV}$	Number of specimens.
1931				
April 28	(·362)	19	(·218)	17
May 5	·046	16	·072	9
May 11	·062	15	·117	10
May 18	·079	14	·073	6
May 26	·186	18	·118	28
June 16	·089	33	·099	44
July 16	·264	8	·226	12
July 22	·158	51	·143	35
August 15	·310	37	·270	45
October 20	·272	22	·263	16
November 25 . . .	·332	22	·312	36
1932				
January 26 . . .	·224	23	·125	25
February 23 . . .	·112	17	·095	7
March 28	·242	23	·316	27
April 26	·121	29	·118	20

* The gonad volume is expressed as ten times the gonad volume divided by the test volume (external).

TABLE III.

SEASONAL VARIATION IN GONAD CONDITION ON THE BREAKWATER.

Date.	Percentages.						Numbers examined.		Percentage of total spent.
	Unripe.	Ripe. ♂	Spent.	Unripe.	Ripe. ♀	Spent	♂	♀	
1931									
March 27	15·7	84·3	–	62·8	37·2	–	51	51	0
April 21	7·7	46·2	46·2	12·5	75·1	12·5	26	8	38·2
April 29	3·1	18·7	78·3	–	42·1	57·9	32	19	70·6
May 5	–	5·3	94·7	–	–	100	19	6	96·0
May 13	–	–	100	–	20	80	9	10	100
May 21	–	–	100	–	20	80	8	5	
June 4	–	–	100	–	–	100	18	29	
June 19	–	–	100	–	–	100	17	33	
July 7	–	–	100	–	–	100	16	43	
October 16	8·4	91·6	–	100	–	–	12	16	
October 20	14·3	85·7	–	100	–	–	14	12	
November 25	5·6	94·4	–	100	–	–	18	18	
1932									
January 26	–	100	–	94·7	5·3	–	30	19	
February 8	–	100	–	50	50	–	28	24	
March 9	–	100	–	4·8	95·2	–	29	21	0
April 4	–	70	30	–	57	43	30	28	36·2
April 5	–	79	21	–	58	42	28	24	30·8
April 13	–	50	50	–	46	54	8	13	52·3
April 18	–	38	62	–	63	37	26	24	50·0
April 25	–	4	97	–	10	90	33	30	93·6
May 2	–	16	84	–	11	79	18	19	81·1

TABLE IV.

SEASONAL VARIATION IN GONAD CONDITION ON THE BREAST.

Date.	Percentages.						Numbers examined.	
	Unripe.	Ripe. ♂	Spent.	Unripe.	Ripe. ♀	Spent.	♂	♀
1931								
April 28	–	–	100	–	–	100	17	19
May 5	–	–	100	–	–	100	43	39
May 10	–	–	100	–	–	100	15	10
May 26	–	–	100	–	–	100	18	27
June 16	–	–	100	–	–	100	28	32
October 20	100	–	–	100	–	–	22	16
November 27	71·5	28·5	–	100	–	–	7	18
1932								
January 26	33·3	66·6	–	100	–	–	21	26
February 24	7·2	92·8	–	100	–	–	14	7
March 28	13·6	86·4	–	66·6	33·3	–	22	27
April 5	–	73	27	–	79	21	33	28
April 13	–	43	57	–	67	33	30	20
April 14	–	60	40	–	54	46	26	25
April 18	–	50	50	–	57	43	16	21
April 21	–	54	46	–	38	62	24	26
April 26	–	42	58	–	54	46	24	33
April 30	–	69	31	–	55	45	29	27
May 4	–	50	50	–	46	54	24	24
May 9	–	60	40	–	64	36	15	31
May 13	–	8	92	–	23	77	25	26

TABLE V.

SEASONAL VARIATION IN GONAD CONDITION ON THE CHICKENS.

PERCENTAGES.

Date.	Unripe.	Ripe. ♂	Spent.	Unripe.	Ripe. ♀	Spent.	Numbers examined. ♂	♀
1931								
May 6	–	–	100	–	66·6	33·3	2	3
May 21	–	42·8	57·2	–	20	80	14	10
May 28	–	60	40	–	–	100	5	10
June 13	–	5	95	–	–	100	20	33
June 25	–	–	100	–	–	100	1	2
1932								
February 17	92·8	7·2	–	82·4	17·6	–	14	17
February 20	–	100	–	80	20	–	3	10
March 9	50	50	–	25	75	–	6	4
March 29	33·3	66·6	–	37·4	62·6	–	12	11
April 16	–	58·7	41·3	–	41·6	58·4	17	12
April 26	–	78·7	21·3	–	73·5	26·5	14	15
May 1	–	75	25	–	40	60	4	5
May 18	–	–	100	–	–	100	12	3

TABLE VI.

SEA TEMPERATURES IN PORT ERIN BAY.

Taken at 9 a.m., being the average temperatures for the weeks ending on the dates given.

1931.		1932.	
February 7	7·3° C.	February 6	8·9° C.
14	7·5	13	8·0
21	6·5	20	7·5
28	7·1	27	7·8
March 7	6·1	March 5	7·3
14	5·5	12	7·1
21	5·9	19	7·5
28	6·5	26	7·8
April 4	5·9	April 2	8·2
11	6·7	9	8·0
18	7·3	16	7·8
25	6·9	23	8·0
		30	8·3
May 2	7·5		
9	7·8	May 7	8·4
16	8·3	14	8·8
23	8·6	21	9·2
30	9·3	28	9·8

ECHINUS ESCULENTUS.

SUMMARY OF GONAD CONDITIONS.

1931.	*BREAKWATER.*	*BREAST.*
April.	Varying from half-full to full. Mostly ripe. Only about 10% unripe. A few spent.	Both sexes either spending or spent. Volumes at a minimum by the end of the month.
May.	None unripe, but rather a mixed sample as to the percentage of spents. Towards the end of the month the gonad volumes are beginning to pick up a little.	Practically all spents, but some relict ova and sperm are to be found.
June.	Mostly spent, and the volume definitely picking up in both sexes. Relict sperm and ova present in some quantities.	Very much as above.
July.	All spent. The gonad volume is rising. Plenty of ripe sperm are still obtainable. The ovaries contain very small ova, and also, in many cases, considerable numbers of relict ova.	The gonads are picking up a little in volume. No spermatocytes could be found, but oocytes were beginning to differentiate, and there were developing ova up to 80μ in diam. in a few cases.
Aug.	The gonad volumes are still increasing. The males still mostly contain some active sperm, though not usually in large quantities. The females often have some relict ova. Large quantities of small ova up to ca. 5μ and smaller numbers up to 50μ. A very few up to 95μ. No sperm morulæ recognised. Female gonads about half full. Males at about their maximum size.	Gonads of both sexes have about reached their maximum size. Ova are up to 80–90μ together with a few relicts. There were a few relict sperm, but no sperm morulæ were seen.
Sept.	Very much as above. Still no sperm morulæ seen. The gonads of the males show no change in volume, but the females are still increasing.	No data.
Oct.	Sperm morulæ abundant, and sperm in some individuals. Males are much the same, but some spermatocytes are to be seen. Females contain all sizes of ova up to 110μ and their volume is still increasing.	Little change in the gonads. There are ova up to 100μ.
Nov.	The males contain large numbers of ripe sperm and also of sperm morulæ. The females have ova up to 145μ and some nearly ripe.	Little change. Ova up to 115μ. Males with abundant sperm morulæ. Some with ripe sperm.
Dec.	No data.	No data.
1932.		
Jan.	The males are nearly all full of ripe sperm, but stages of spermatogenesis are probably also present. The male gonad volumes are dropping slightly. One or two females were ripe, and a number contained up to 50% of ripe ova. The female gonad volumes were still rising.	A fair proportion of the males were ripe, many with stages of spermatogenesis. showing. Some of the females contained large ova, but none were ripe. Gonad volumes were dropping in both sexes.
Feb.	Males all ripe and full, and their volume dropping slightly. Female gonad volume still rising. About 50% of the females were ripe, and the rest mostly contained some ripe ova.	The gonad volumes of both sexes had dropped considerably further. Most of the males were ripe. No females were ripe, though there were ova up to 150μ and a few ripe ova.
March.	All the males, and nearly all the females were ripe, and spawning was commencing. The male gonad volume dropped slowly in the beginning of the month while the female was coming to its maximum. Later both dropped sharply.	The gonad volumes rapidly picked up again. Most of the males were ripe, and some few females. The rest of the latter were approaching ripeness.
April.	Most of both sexes have spawned by the end of the month.	Spawning in progress throughout the month, and the gonad volume dropping correspondingly. Still a small proportion of unripe specimens in both sexes.
May.		Spawning practically completed by the end of the month.

Observations on the Growth of the Claspers and Cloaca in *Raia clavata* Linnaeus.

By

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With 7 Figures in the Text.

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I. INTRODUCTORY.

In the course of work on the life-history and biology of the Raiidæ in the English Channel, and especially of *R. clavata*, the most important species commercially (**4**, p. 9 *et seq.*), it has been found necessary to attempt to disentangle the migrations of sexually mature fishes from those of juvenile individuals by means of marking experiments. In both sexes sufficiently small individuals could with safety be written down as juveniles and the largest of both sexes as adults. There remained, however, a considerable but ill-defined range of sizes (different in the two sexes) within which might be found fishes of all stages—juveniles, adolescents and adults.

In dealing with male fishes this difficulty was overcome by noting the size and condition of the claspers. In the female, however, the writer was not aware of a corresponding—or any other—external feature from which could be deduced with reasonable accuracy *in a live fish* her state of sexual development. The present investigation was undertaken, therefore, in order to discover whether or not such a feature existed. Attention soon became directed to the greatly accelerated relative growth rate in the cloaca of adolescent fishes and the relatively much greater length of this organ in mature than in juvenile individuals.

During this adolescent period of greatly accelerated growth in length, the cloaca also changes markedly in shape, becoming very much widened out, especially at its inner end (*cf.* Figs. 4 and 5). These changes in the size and shape of the cloaca are so extensive as to be easily discernible by digital examination. There is thus available in the female as well as in the male a ready means of ascertaining the sexual condition of the live fish. This method is now being applied in all further Ray-marking experiments.

The results of detailed observations on these changes in the growth of the claspers and cloaca in *R. clavata* form the substance of this paper.

II. The Claspers.

All species of Rays and Skates (Raiidæ) exhibit well-marked sexual dimorphism. Some of the secondary sexual characters, such as the presence of alar and malar spines and more pointed teeth in the male, become obvious only in sexually mature or nearly mature individuals. The presence of claspers in the male can be detected, however, at a very early stage of development. Thus, during at least the latter part of their embryonic development within the egg, and throughout the entire post-embryonic life of these fishes, the presence or absence of claspers forms a ready means of distinguishing male from female. In addition to their being the most characteristic and most easily discernible feature of the male fish, the claspers serve also, better than any other externally evident character, as an index of his state of sexual development. During the entire period of juvenile growth, before the onset of adolescence,* the claspers remain relatively small and inconspicuous, so much so that they may be entirely invisible from the dorsal side being shorter than, and hidden by, the pelvic fins. But at the onset of adolescence the claspers suddenly begin to grow very rapidly, and their tips soon extend backwards far beyond the limits of the pelvic fins.

This sudden change in the size and condition of the claspers was long ago noticed by ichthyologists. In the year 1877, for example, Malm (**3**, p. 607) stated that in a male *R. clavata* 216 mm. long the claspers were only about 3 mm. in length. In 1895 Fries (**2**, p. 1106) wrote that in a male of this species about 45 cm. long the claspers were " still quite small and short, their tips extending only a little more than half-way along the ventral fins." In a specimen 52 cm. in length he records that the circumstances were " essentially the same " except that the claspers were just a little longer in relation to the fins. But in an individual " rather more than 60 cm. long " Fries remarks that the claspers were so well developed that their tips extended back to more than half-way along the length of the tail.

In order to follow more closely these changes in the relative growth rate of the claspers, measurements have been made on representative samples of male *R. clavata* at all sizes from recently-hatched individuals upwards to the largest obtainable. In recording the lengths of the claspers, for the sake of uniformity all measurements have been made on the left clasper. The length has been taken as the distance between the tip of the clasper and its point of emergence from the skin on the inner side (Fig. 1). This point is sometimes not well defined in adult fishes with large claspers, and exact measurements are not with them possible. A small part of the variation in recorded clasper lengths of adult fishes must be ascribed, therefore, to the action of this purely extrinsic factor as well as to the individual variations in size and body-proportions which are always found in the separate representatives of every animal (and plant) species.

---

* The post-embryonic life of a Ray is very clearly divided into the usual phases: (1) the *juvenile* phase, during which the fish simply grows in size; (2) the *adolescent* phase, during which fundamental changes take place very rapidly and bring the individual to puberty; (3) the *adult* (sexually mature) phase.

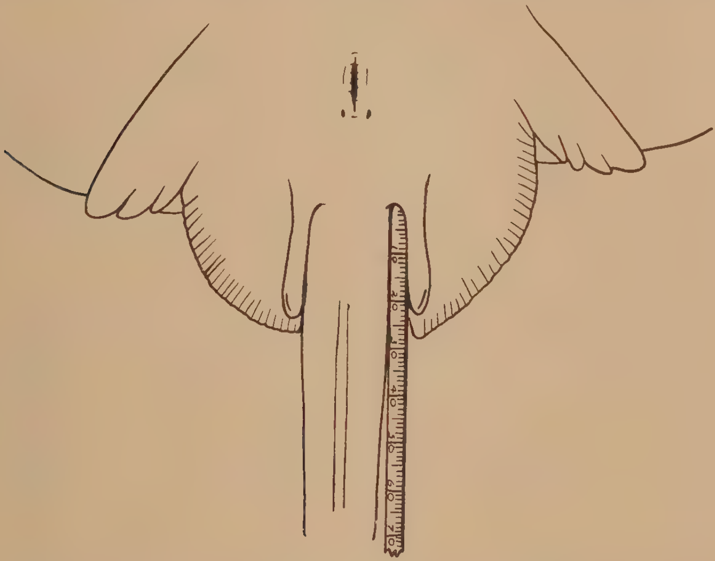

FIG. 1.—*R. clavata*—juvenile male ; 31 cm. disc width ; clasper 22 mm. × $\frac{2}{3}$.
(See text.)

It is found that throughout the immature stages of development the claspers grow slowly and regularly, their length at any time during the juvenile phase showing a linear correlation with the total size of the fish, as expressed, say, by width of disc ; that is to say that points representing the length of the clasper at different times during the juvenile growth period plotted against the width of the disc fall upon a straight line. This is well shown in Figure 2. Each plotted point indicates the mean value of numerous clasper measurements in centimetre size-groups of fishes. The lengths of the vertical lines drawn through those points indicate the ranges of the measurements from which the means were drawn.*

It will be seen that for fishes up to and including the 43-cm. size-group the mean values lie very closely along the straight line *ab*, the correlation equation for which is

$$Y=0{\cdot}993\ X-5{\cdot}596$$

where Y=length of clasper (in mm.), and X=width of disc (in cm.). In succeeding size-groups the ranges of clasper length measurements show progressive extension in an upward direction and the mean values rise rapidly above the line *ab*. This means that in some fishes the claspers are now exhibiting a greatly accelerated relative growth rate.

In size-groups 50 cm. to 54 cm. (inclusive) disc widths, the ranges of clasper lengths reach and retain maximum values, these organs now having attained the fully adult size in some fishes while in others they still remain in the juvenile condition. Examination of Figure 2 clearly shows that the onset of the change in relative growth rate of the claspers, with which are correlated all the other phenomena of adolescence, does not always take place in all fishes at the same size. In some this change takes place when they have attained a disc width of round about 44 cm.; in others it is delayed until a much larger size is reached.

In Figure 3 these results, for the larger fishes, are shown graphically in a different manner which brings out this point more fully. Here the length of the clasper in individual fishes of 5-cm. size-groups, from 36 cm. in width of disc upwards, is indicated by the position of a dot. In the smallest size-group represented—36–40 cm. disc widths—all the claspers are still short and the range of recorded lengths is small. In the size-group next above—41–45 cm. disc widths—most of the fishes still have short claspers, but a few have entered the adolescent phase and are showing increased relative growth rate of this organ. In the size-group next higher again this process has proceeded still farther and one individual has actually become fully mature.

The size-group 51–55 cm. disc widths is of particular interest. Here the clasper length measurements show two distinct modes—one at the lower end of the range, produced by fishes which are still in the juvenile phase, and one at the upper end of the range, produced by fully adult individuals.† The approximately symmetrical bi-modal curve produced by the clasper length measurements of this group confirms the conclusions to be deduced from analyses of the complete data presented in Figures 2 and 3. These are :—

(1) that, in the English Channel area, in any sample of male *R. clavata*

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* Mean values for those size-groups which include adolescents and later stages are without significance and are not shown.

† Shortest clasper found in a fully mature male—176 mm. (*vide* dotted line, Figs. 2 and 3).

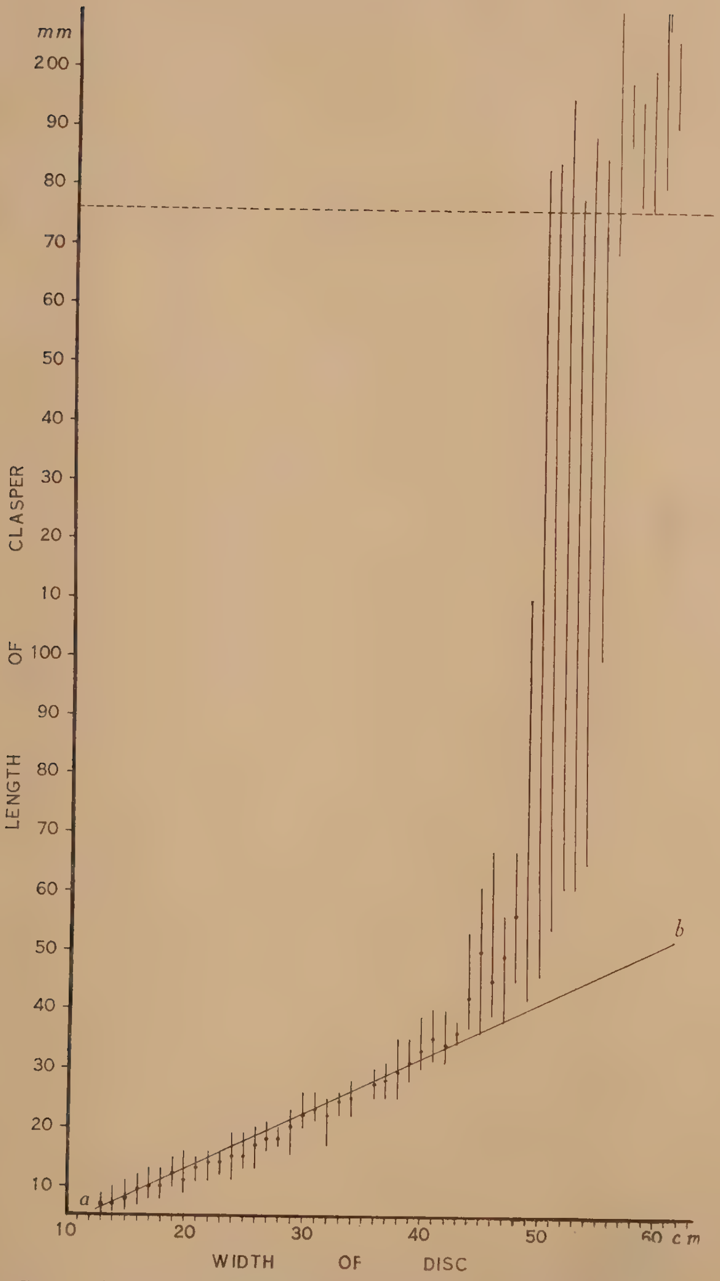

FIG. 2.—*R. clavata*—clasper length plotted against disc width in centimetre size-groups. (For explanation see text p. 889.)

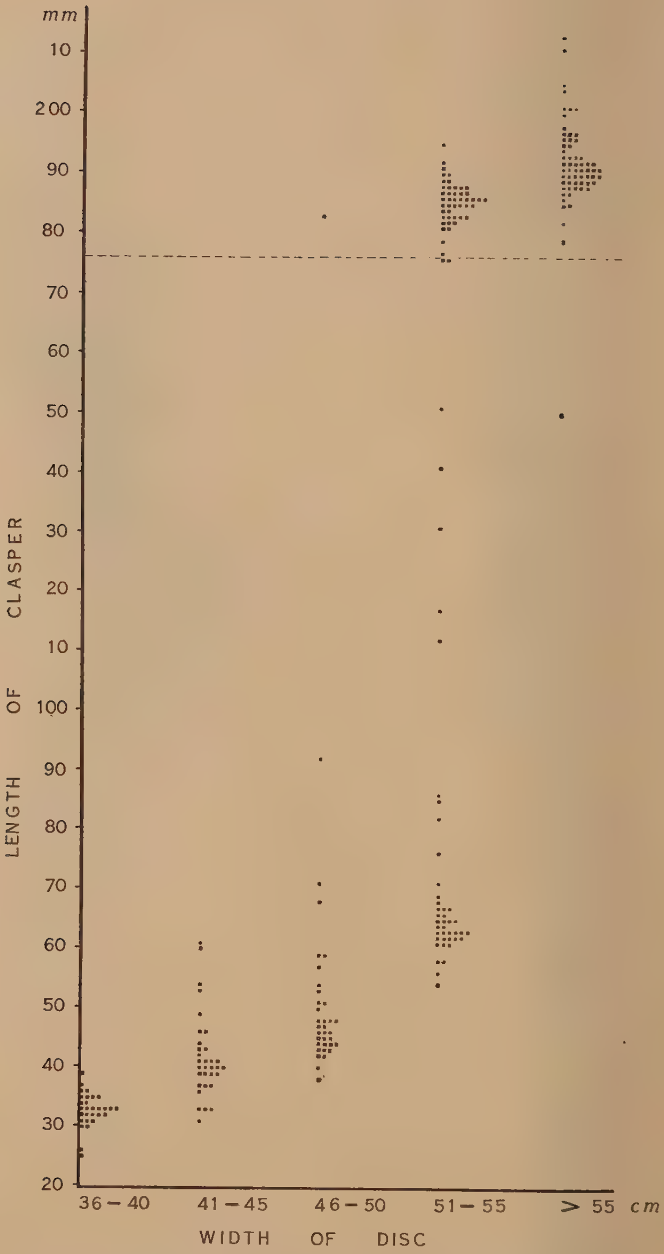

FIG. 3.—*R. clavata*—clasper length plotted against disc width in 5 cm. size-groups. (For explanation see text p. 890.)

in which no fish exceeds about 50 cm. disc width, the great majority of the individuals will be immature juveniles. This will hold true whether the sample be restricted to any arbitrary size-group of small range or consists of fishes at all sizes up to 50 cm. (about) disc width. Over most of this range samples of restricted size-groups will consist of 100 per cent juveniles, but samples at or near its extreme upper limit will contain a certain proportion of individuals at more advanced stages.

(2) that, similarly, in any sample which includes no fishes of less than approximately 56 cm. disc width, the majority of the individuals will be mature adults.

(3) that, in any representative sample of male fish of size-group 51–55 cm. (inclusive) disc widths, juveniles and adults will tend to be equally represented, while adolescents at all intermediate stages will also be found.

III. THE CLOACA.

The cloaca of the female Ray exhibits growth phenomena very similar to those found in the claspers of the male, and cloacal measurements have been made on individuals at all stages of growth. The distance from the anterior edge of the cloacal opening to the anterior end of the cloaca (in the middle line) when in normal extension, has been used as the measure of cloacal length. This measurement is made by opening the abdominal cavity and placing the tip of one finger of the left hand against the anterior end of the cloaca as it lies in position. At the same time a not too sharply pointed rod, graduated in millimetres, is inserted into the cloacal aperture and pushed forward until it presses against the left-hand finger. The length of the cloaca is then read off where the anterior edge of the cloacal external opening crosses the rod (Figs. 4 and 5).

Throughout the juvenile phase the cloaca grows only slowly and, like the clasper of the male, preserves a linear correlation between its length and the body dimensions of the whole fish. In Figure 6 the cloaca lengths in fishes of centimetre size-groups are plotted against disc widths. For fishes up to and including the 59-cm. size-group the mean values lie very closely along the straight line *ab* whose correlation equation is

$$Y=0{\cdot}574\,X-2{\cdot}175$$

where Y=length of cloaca (in mm.), and X=width of disc (in cm.). In fishes over this size the cloaca shows greatly accelerated relative growth rate in many individuals and the range of cloacal length measurements increases enormously, reaching and retaining maximum values in fishes of about 67–76 cm. (inclusive) disc widths.

In Figure 7 the length of the cloaca in individual fishes of 5-cm. size-groups, from 36-cm. disc width upwards, is plotted. In this figure the cloacal length measurements produce an approximately symmetrical bi-modal curve in the size-group 66–70 cm. disc widths. From perusal of Figures 6 and 7, therefore, the following conclusions can be drawn concerning the females of *R. clavata* in the English Channel area :—

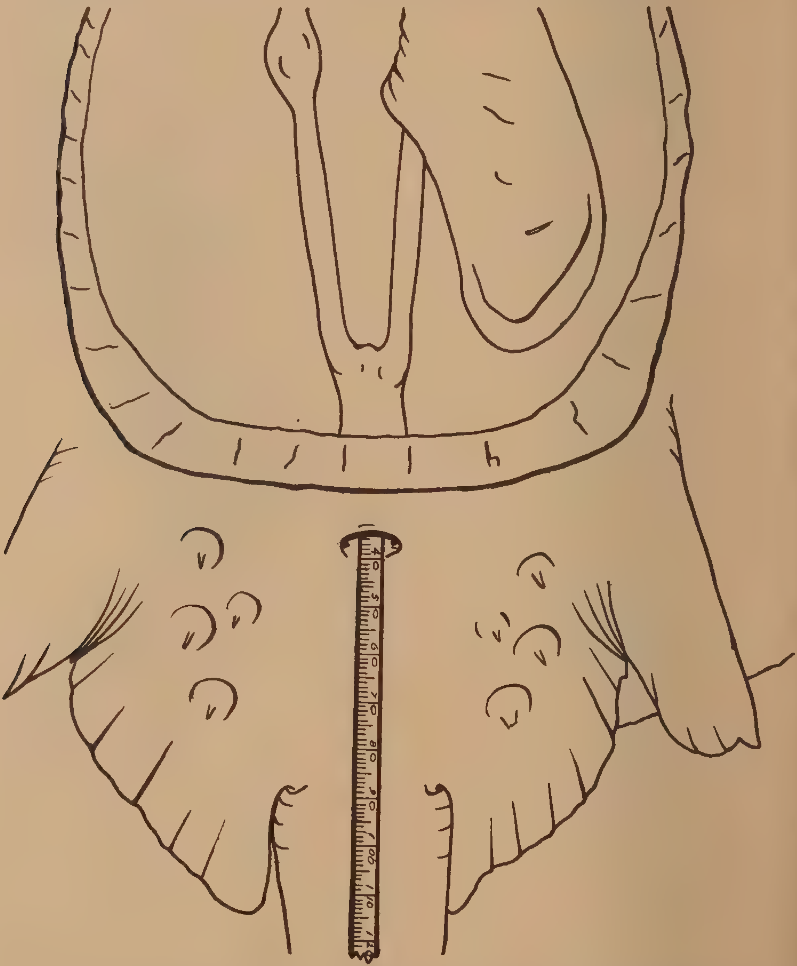

FIG. 4.—*R. clavata*—juvenile female ; 65 cm. disc width ; 36 mm. cloaca length. Dissected to show cloaca. Note immature left ovary (left *in situ*), and small shell gland. ×⅔. (For further explanation see text pp. 887 and 893.)

(1) that in any sample of female fishes of this species in which no individual exceeds about 65 cm. in width of disc the great majority will be immature juveniles. This will hold true whether the sample be restricted to any arbitrary size-group of small range or consists of fishes

at all sizes up to the 65 cm. (maximum) disc width. Over most of this range samples of restricted size-groups will consist of 100 per cent juveniles, but samples at or near its extreme upper limit will contain a certain proportion of individuals at more advanced stages.

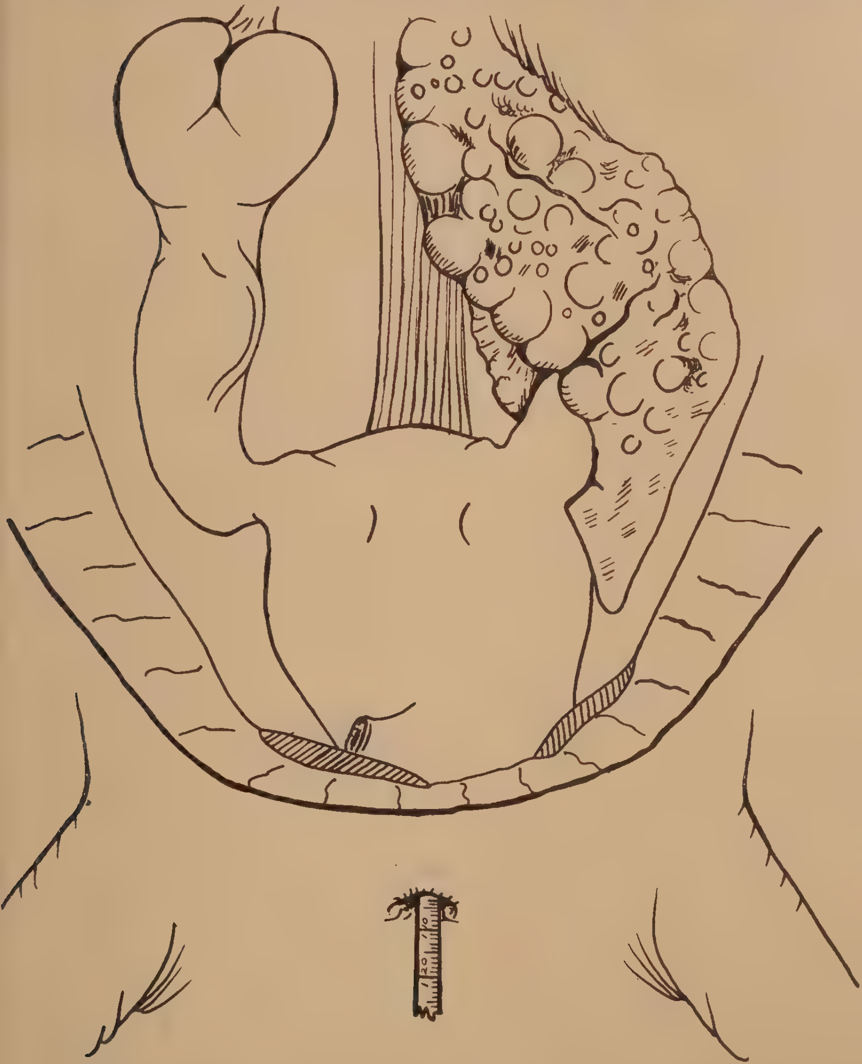

Fig. 5.—*R. clavata*—mature female; 72 cm. disc width; 102 mm. cloaca length. Dissected to show cloaca. Note also developing eggs in ovary and large shell gland. $\times\frac{2}{3}$. (For further explanation see pp. 887 and 893.)

(2) that, similarly, in any sample which includes no fishes of less than approximately 70 cm. disc width, the majority—but not all—of the individuals will be mature adults.*

(3) that in any representative sample of females of size-groups 66–70 cm. (inclusive) disc widths, juveniles and adults will tend to be equally represented, while adolescents at all intermediate stages will also be found.

In the course of this work, the possibility that, after all one season's eggs have been deposited, the cloaca may return to its virgin condition has not been overlooked. But the fact that the range of cloacal length measurements in all fishes of 76 cm. and upwards in width of disc is relatively small, grouped around a mean value of about 100 mm.—a figure far removed from that which would be expected in virgin females of those sizes—suggests very strongly that this does not happen. This conclusion is further supported by these additional observations. On Newlyn (Cornwall) fishmarket, in September, 1932, the plan was adopted of trying to find a fish of 76 cm. disc width or over with a small cloaca of say 50 mm. length or less. Though many hundreds of fishes were examined, including a large number with fully spent ovaries, the shortest cloaca length

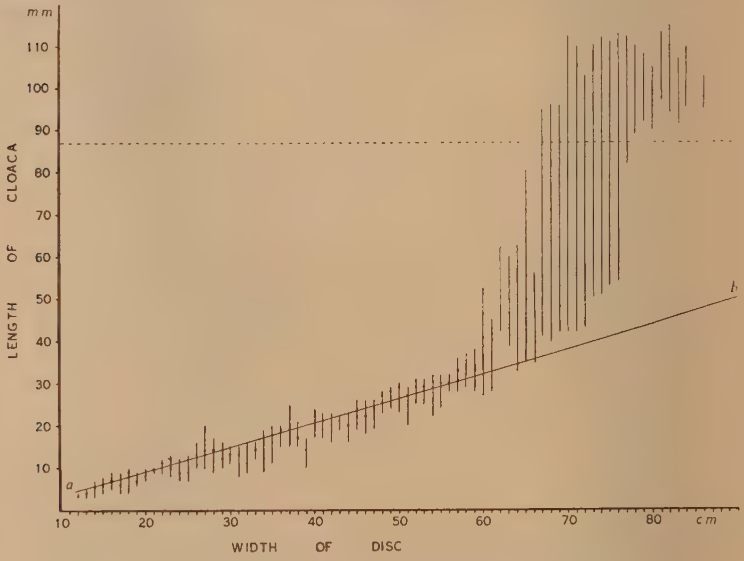

FIG. 6.—*R. clavata*—cloaca length plotted against disc width in centimetre size-groups. (For explanation see text p. 893.)

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* Shortest cloaca length recorded in a fully mature fish—87 mm. (*vide* dotted line, Figs. 6 and 7).

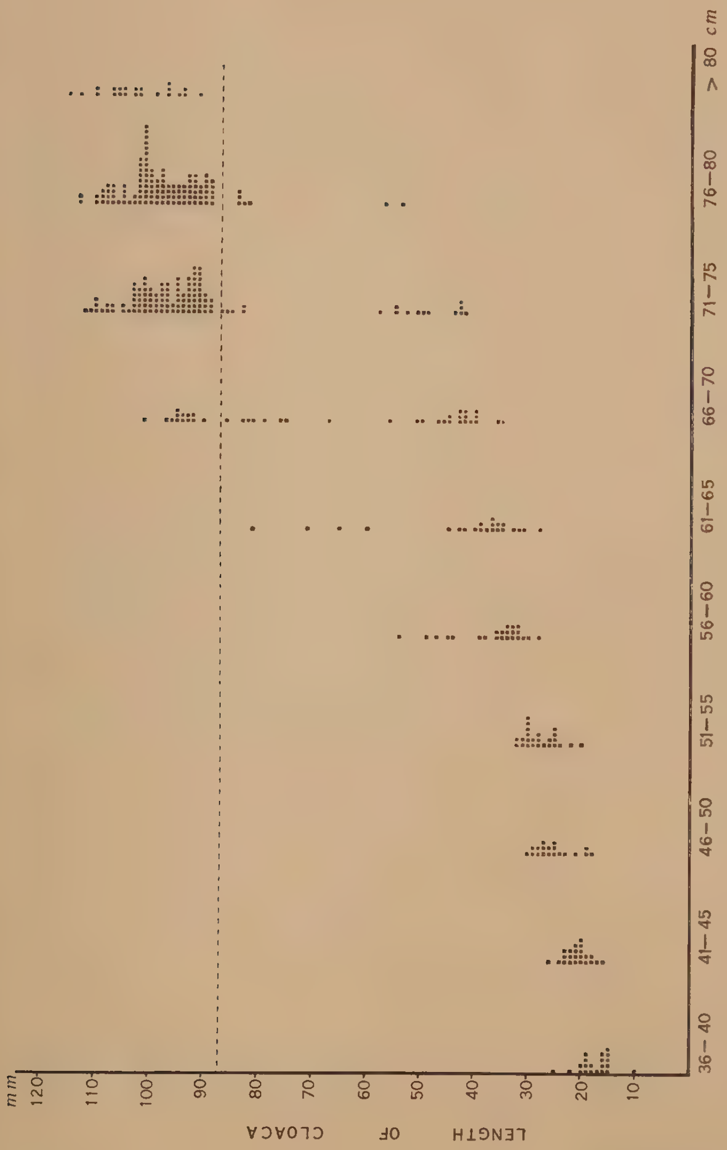

Fig. 7.—*R. clavata*—cloaca length plotted against disc width in 5 cm. size-groups. (For explanation see text, p. 893.)

recorded was 87 mm. This was in a gravid female of 76 cm. disc width and containing in each uterus an egg ready for deposition.

IV. Practical Applications.

A. It will be seen from Figure 2 that the 44-cm. (centimetre) size-group of male fishes contains the smallest individuals which show unmistakable acceleration in the relative growth rate of the claspers, thus indicating that they have entered the adolescent phase. The 50-cm. (centimetre) size-group contains the smallest fishes which have become fully mature.

It may with safety be assumed that the first (smallest) fishes to enter the adolescent phase will be also the first (smallest) fishes to reach puberty. It would thus appear that in the males of this species, the adolescent phase occupies roughly the time required to grow round about 6 cm. in width of disc.

Now the results (unpublished data) of the marking experiments so far carried out (*vide* p. 1) indicate that the adolescent males of *R. Clavata* grow at the rate of from about 3 cm. to 5 cm. disc width in the course of one annual growing period. The experiments are being continued and full details will be published in a subsequent paper. But sufficient data have already been collected to suggest that the above figures are reasonably reliable. If this be so, it would appear that in the males of this species the adolescent phase normally occupies rather more than one and not more than two growing periods. From this it may reasonably be concluded that these fishes enter the adolescent phase during one growing period and reach puberty during the growing period of the following year, the time occupied by the changes extending over part or all of the two periods.

In the females (Fig. 6) the difference in size between the smallest fishes to enter the adolescent phase and the smallest to reach puberty appears to be most frequently about 7 cm. disc width. Although females grow rather more rapidly at this stage than males, this difference in size represents in them too the growth increment of more than one and not more than two growing periods. The period of adolescence would appear, therefore, to be the same in both sexes.

B. It has been recorded in a previous paper (**5**, p. 617) that, on certain fishing grounds near Plymouth, there is in the spring months of every year, a congregation of large and fully mature Thornback Rays. At the same time that these adult fishes are being landed by fishing boats using fixed nets, other landings are being made by vessels using long lines or " boulters " on different grounds in the vicinity. A marked feature of the fishes caught on these lines at this time is that they frequently contain a high proportion of adolescent individuals. As with the adults from the nets (**5**, p. 617), so also with these adolescents, a landing will often consist almost entirely of one sex, either male or female. From consideration of the data set forth above it seems likely that these adolescent fishes, typical of " boulter " landings in the spring, entered the adolescent phase during the growing period of the previous year and that the majority, at any rate, of the year-class to which they belong will reach puberty during the growing period immediately following -i.e. later on in the same year. By the ensuing spring these young adults will have joined the shoals of mature fish which will populate the fixed-net fishing grounds at that time.

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A Comparative Study of *Metridium senile* (L.) var. *dianthus* (Ellis) and a Dwarf Variety of this Species occurring in the River Mersey, with a discussion on the Systematic Position of the Genus Metridium.

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With 5 Figures in the Text.

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INTRODUCTION.

The anemone at present under consideration resembles *M. senile* (L.) var. *dianthus* (Ellis) in many respects but shows certain differences. It was for a time provisionally regarded as *M. senile*, but the body wall is thinner than in this species, sexual maturity is attained at a very small size and the disc is rarely distinctly lobed. The subsequent discovery of an abundance of penicilli in the acontia led one to think that the Dingle anemone was perhaps a Sagartia and not a Metridium. Living specimens were then sent to Professor Stephenson who identified them as one of the small local atypical forms of *M. senile* which occur in the intertidal regions of many parts of the British coasts. It is not known whether all these forms are simply varieties or whether on further investigation some of them might be justly ranked as species. The present research was undertaken with a view to solving this problem in the case of the Dingle anemone.

All sizes and all colour varieties of *M. senile* were obtained either from Plymouth or Port Erin for comparison with the Dingle form. Observations have been made on the external features and the stinging cells of specimens from these three localities along with an investigation of the anatomy of the Dingle form.

THE DINGLE ANEMONE.

HABITAT.

The anemone occurs on the river side of the revetment to the north of the oil jetty, Dingle, River Mersey (**1**, Fig. 1). Many individuals are attached to a mooring chain and other large colonies occur on the adjacent rocks. Only at extreme low water can one be sure of collecting specimens, since average tides fail to expose them.

The revetment is a low bank which lies parallel and close to the shore. It consists of large loose stones, rough with barnacles and covered with a thick deposit of fine mud. The water here is brackish and particularly foul because of the abundance of silt, the presence of an oil jetty, and a sewer in the vicinity. Often, when collecting, the water was seen to be covered with a film of oil. The average salinity of the river at Dingle is recorded by Fraser (unpublished records, 1931) as 13°/$_{oo}$ at Low Water and 20°/$_{oo}$ at High Water and the pH as about 7·9.

Large colonies of the more typical *M. senile* are found about three miles down the river on a wooden jetty situated at the north end of the Princes Landing Stage. Here, Fraser gives the average salinity as somewhat higher than at Dingle (23–28°/$_{oo}$ in summer and 21–27°/$_{oo}$ in winter), but the pH value as about the same. These latter colonies are not specially dealt with in this paper.

COLOUR VARIETIES, SIZE, AND HABITS.

There are four colour varieties of the Dingle anemone, salmon pink, white, olive-brown, and grey; the latter two are rare. All the individuals are small; the base of the largest one collected measured only 2·5 × 3·5 cm. and the diameter of the expanded disc rarely exceeded 2·5 cm.

Reproduction occurs by basal laceration and by the deposition of ova. Both these methods are recorded for *M. senile* (**2** and **3**), and its closely allied American forms (**4**). Laceration takes place in the ordinary way by tearing. Figure 1 shows a Dingle specimen with buds produced by this method in the laboratory between 17.9.32 and 22.12.32. It was given frequent changes of sea-water and fed with portions of Mytilus which were

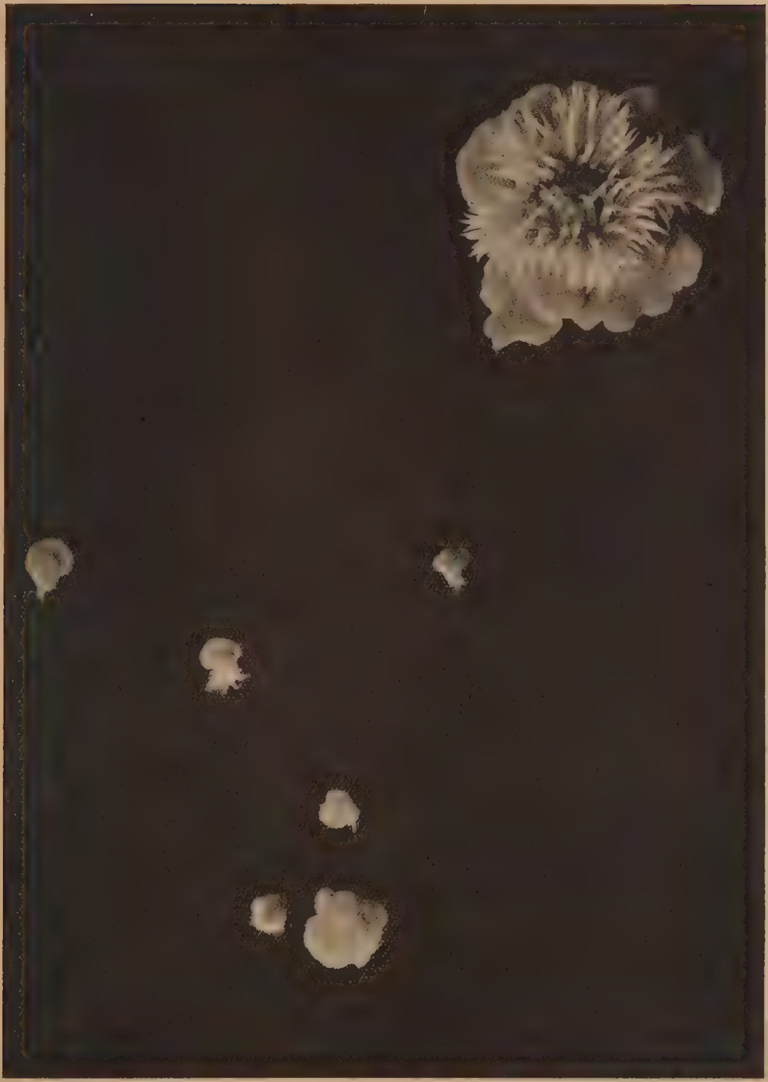

FIG. 1.—A Dingle anemone with buds produced by basal laceration. × 2. Photograph by P. Bond.

ingested, and with Nitzschia culture. Two individuals kept in captivity by Professor Orton from 5.6.30 to 5.11.30 together produced 34 buds. In this case the adults were not fed, but they were kept clean and the water was changed frequently. They were perfectly healthy.

Laceration appears to be of frequent occurrence in the Dingle anemones in their natural habitat; they often have a very irregular and sometimes torn basal outline. It has been shown in Sagartia and other anemones that the roughness and smoothness of the substratum has little or no effect on the rate of reproduction by this method (**2**). The observations of Torrey (**5**) on *M. fimbriatum* Verrill, suggest that one might possibly attribute the frequency of this process to the uncongenial habitat at Dingle. He concluded from his experiments that the mode of reproduction may be influenced by the environment. Only on one occasion did he observe basal laceration in the natural habitat, all other examples occurred in anemones which had been kept for several months in aquaria where the conditions were not so favourable. Wider observations may however show that lacerations are commoner in the field than is here suggested.

Basal buds have been seen in the Dingle anemones; they are also recorded in *M. senile* (**3**) and *M. fimbriatum* (**5**). They are probably incompletely lacerated portions of the base which have already developed tentacles, since true budding is of doubtful occurrence among the Actiniaria (**2**). No œsophageal buds such as are described in *M. fimbriatum* have been seen in the Dingle form.

Sexually mature individuals may be found in June, but the duration of the breeding season is unknown. The few available records of the spawning of *M. senile* give its breeding season from March to September although they also suggest a variation in the period according to the locality. The Millport specimens breed from March to June (**6**), whereas the Plymouth records (**7**) are from August to September. Two spawning females of the Dingle anemone were observed by Professor Orton in June, 1932. The eggs ranged from 110-130μ in diameter. Their size differs somewhat from the measurements of the eggs of *M. marginatum* (**8**) and *M. senile* (**9**), but the few observations on the eggs of the latter indicate a considerable amount of variation in their size. Gemmill (**9**) records an average diameter of 0·1 mm., but 105 eggs of a large brown specimen from Plymouth which spawned overnight in the laboratory at Liverpool on 11.11.32 had an average diameter of 173·6μ.

Sexual maturity at a small size is one of the most interesting features of the Dingle anemone. Observations on the smallest size at which *M. senile* var. *dianthus* is mature do not appear to have been made apart from Elmhirst's record. I am indebted to him for his information about the Millport specimens. Spawning does not take place, as far as he can recall, until the animals are approximately 2″ in height when expanded.

They are therefore at least twice as large as some of the ripe Dingle anemones.

When kept in finger bowls, the Dingle specimens frequently creep up the sides of the vessel until they are partly exposed to the air, a habit which they share with *M. senile* (**3**). Both young and adults possess the capacity of floating upside down beneath the surface film, although this position was only observed when the water in the bowls required renewal. In each case the animal crept up the side of the bowl to the water level, slowly released its hold and finally floated off. Sometimes a delicate horny, brown membrane covered the base. The base of such individuals frequently has a silvery appearance which one may possibly attribute to the enclosure of air between the membrane and the true base. This observation recalls the interesting modification met with in the floating Minyads, which have a hollow base containing a horny float from which the anemone is suspended head downwards.

A COMPARISON OF *M. SENILE* (L.) VAR. *DIANTHUS* (ELLIS) WITH THE DINGLE ANEMONE.

(*a*) *The external features and anatomy.*

Anatomical investigations have been made to determine the characters of the Dingle anemone for comparison with those of *M. senile.* Only the salmon-coloured anemones were used. Dissections, and hand sections of material fixed in either formalin or Bouin's fluid and frozen in a solution of gum arabic were made to study the grosser anatomical features. Serial sections of material embedded in paraffin wax and stained in borax-carmine and picro-indigo-carmine were used to study the finer characters.

The results of these investigations and a careful comparison of the external features of the Dingle anemone with the accepted descriptions of *M. senile* (**3**, **10**, **11**, and **12**) indicate a very close resemblance between these two forms, but also certain differences. The general appearance of the Dingle anemone differs in some respects from the typical adult *M. senile ;* the column is often short, although it sometimes forms quite a tall pillar ; the base is broad, spreading, with an irregular outline as in some Sagartias and a diameter usually greater than the height of the column. The scapus wall is thinner and more translucent than in the typical form. Maybe, as has been suggested by Fraser (unpublished records, 1931), its different texture is due to the low salinity of the water at Dingle. In the number of tentacles and the frequent absence of clear disc lobes, the Dingle anemone resembles the young of *M. senile* rather than the adult. Individually, the above features may not be very significant, but together they give the living anemone quite a different facies from the type form. The same colour varieties and colour pattern are met with in both anemones. They are identical in the structure of their mesenteries and cinclides and in the form and distribution of the musculature of the tentacles, disc, and scapus. They both exhibit fluctuations in the number of their perfect mesenteries. The European *M. senile* and the American species of Metridium are often hexamerous, but specimens of the former are recorded with 6 11 pairs of perfect mesenteries and of the latter with 4–15 pairs. In thirty-three examples of the Dingle anemone their numbers were as follows :—

No. of pairs of perfect mesenteries.	11	10½	10	9	8½	8	7½, ½	7	6½	6	5½	5	4
No. of individuals	2	1	1	1	3	8	1	5	1	3	2	4	1

The sections of the specimens with five and ten pairs were incomplete, so that it is possible that they possessed more than this number.

A detailed study of the variation in the number of perfect mesenteries in the European *M. senile* does not appear to have been made, but this aspect of the American representatives of the genus has been the subject of various papers. A brief consideration of these is not irrelevant here, more especially as *M. fimbriatum* Verrill and *M. marginatum* Milne-Edwards are regarded as synonymous with the European *M. senile* (L.) var. *dianthus* (Ellis), (**5**) ; absolute agreement between them is, however, not yet certain (**17**).

Torrey (4), after working on *M. fimbriatum*, concluded that basal fragmentation was especially interesting as a factor affecting the variation in the number of mesenteries and siphonoglyphs. Experiments have shown that monoglyphic and diglyphic polyps can each give rise asexually to both kinds of buds and that the number of siphonoglyphs depends upon whether or not a detached fragment contains a portion of the parent directive system (**13**). In the majority of regenerating fragments, a pair of directive mesenteries is developed from the torn part of the body wall. If a portion of the parent directive system is also present, then a diglyphic polyp with two pairs of directive mesenteries is produced, if not, a monoglyphic form with one pair of directive mesenteries. Hahn and Torrey's experiments demonstrate that there is a definite, but not absolutely strict correlation between the mode of reproduction and the morphology of the polyp. It is considered that sexual reproduction more frequently gives rise to regular diglyphic individuals and laceration to irregular monoglyphic ones. It is probable, therefore, that the predominance of forms with an irregular number of mesenteries among the thirty-three specimens specially examined from Dingle may be attributed to the asexual mode of reproduction.

Perfect agreement has been demonstrated regarding the number of siphonoglyphs and the number of pairs of directive mesenteries (**4**) and (**10**). The variation in their number has not been particularly studied in the Dingle anemone, but twenty specimens which were examined proved to be monoglyphic with one pair of directives. It is interesting to note the variation in the percentages of monoglyphic and diglyphic polyps from various American localities (**13**). The different values may possibly be attributed in some measure to the environment. Unfortunately, the habitat is not described for all the localities which have been studied, but in each there is a greater percentage of the monoglyphic type. Assuming that basal fragmentation is correlated with an unfavourable environment, then one would expect a predominance of monoglyphic specimens at Dingle, since the chances of a detached fragment containing a portion of the parent directive system are fewer than it not containing a piece. It would be interesting to compare the percentages of monoglyphic and diglyphic polyps at Plymouth, Port Erin, and Liverpool.

The arrangement of the imperfect mesenteries in the genus Metridium is also very variable (**14**). In some of the Dingle anemones there were only two cycles of imperfect mesenteries with well-developed retractor muscles and mesenterial filaments: three such cycles are present in the young *M. senile* (**11**). This character is probably of little importance in comparing these anemones since it varies with the age of the individual.

Single unpaired mesenteries occur in the Dingle anemones: a similar condition is recorded for *M. senile* (**10**) and *M. marginatum* (**14**). In all these forms one sometimes finds a union of the free edges of two adjacent mesenteries belonging to different mesentery pairs. Irregular specimens of *M. marginatum* and certain of the Dingle anemones agree in their tendency to concentrate the non-directive perfect mesenteries at one end of the actinopharynx.

The majority of the mesenterial filaments in the upper part of the column of the Dingle anemone have a typical trefoil appearance when viewed in transverse section. Their shape agrees fairly closely with the filament of *M. senile* (**11**, Fig. 20), but the lobes are frequently more distinct and the reticulate region better developed. Occasionally a 4 or 5-lobed appearance is presented. One may agree with E. M. Stephenson (**11**) that the specific value of the shape of the mesenterial filaments when viewed in transverse section is not yet fully understood, as a sufficient number of individuals of any one species has not been investigated.

The genus Metridium has in the past been defined as having the gonads on the imperfect mesenteries. Carlgren (**10**) and Professor Stephenson (letter to the author, 8.2.33) record examples in which gonads were present on some of the perfect mesenteries also, the former author stating that when there are more than six pairs of perfect mesenteries, gonads may occur on the additional ones. The Dingle anemones with an irregular number of perfect mesenteries may have gonads developed on some of them. A fertile specimen with only six pairs of perfect mesenteries was not found.

The inferences of importance which may be drawn from the above discussion of the mesenteries and their associated structures are :—

1. The number of perfect mesenteries present in the European *M. senile* and in the American species of Metridium is variable. A knowledge of the number of perfect mesenteries present in a particular individual cannot therefore be used as a reliable character for its identification.

2. Environment may influence habit, and cause changes in the morphology of the genus Metridium. Uncongenial surroundings possibly stimulate reproduction by basal laceration whereby polyps with an irregular number of perfect mesenteries and a varying number of siphonoglyphs are produced, although an irregular number of mesenteries is more frequently associated with the monoglyphic than with the diglyphic condition.

3. There is a definite, but not absolutely strict correlation between the mode of reproduction and the morphology of the individual. Egg embryos as a rule give rise to regular polyps while reproduction by basal laceration is the principal contributory factor to the production of irregular ones.

4. In the typical adult *M. senile* the perfect mesenteries are sterile and the gonads occur on the imperfect mesenteries. When more than six pairs of perfect mesenteries are present, some of them may develop gonads.

(*b*) *The Nematocysts.*

The nematocysts of the Dingle anemone are one of its most interesting features. It possesses all the characters of the Metridiidæ (**15**), but it has an abundance of both spirulæ and penicilli in its acontia, a character which, according to the latest classification (**16**), immediately removes it from this family. Special care was taken when removing the acontia to prevent them from touching any other tissues. The acontia were cut off with clean instruments as soon as they were extruded through the cinclides or mouth so that there was no possibility of contact with cut tissues. Portions were then finely teased in sea-water, mounted either unstained or stained in 1% acid fuchsin, and examined with a 1/12th objective. A pure sample of the acontia cannot however be guaranteed since sooner or later in their ordinary life they are bound to be contaminated with the nematocysts from the mesenterial filaments and the ectoderm.

The acontia of at least thirty individuals have been investigated. They all contained both types of nematocyst. The spirulæ were most abundant, but the penicilli were always plentiful and one was sure of finding them in any preparation of a fragment of an acontium. The two types are quite distinct when they are exploded. The spirulæ are identical with those described for *M. senile* (**16**, Fig. 1). The penicilli (Fig. 2) are of the bottle-brush type. The majority have a blunt tip, but I suspect that a few may have a short, fine, terminal thread. The average size, length and breadth of the spirula and penicillus capsules is given in Table I. Their size shows only minor fluctuations between anemones of approximately equal sizes.

A very careful search was then made for penicilli in the acontia of *M. senile* var. *dianthus* from Plymouth, Port Erin, and the Princes Landing Stage, Liverpool. They were found to be universally present in quite considerable numbers in all the small specimens which were examined from each of these localities (see Table I), although they were not so abundant as in the Dingle anemones. They occur in the white, grey, orange, and brown colour varieties. In large specimens they are sparse and sometimes absent. Since these results were obtained, Carlgren (**17**, 1933) has recently recorded the presence of a few penicilli in young specimens but has failed to find them in the adults.

The spirulæ and the penicilli from the acontia of the Dingle anemone have much the same range in size as in *M. senile* (see Figs. 4 and 5, pp. 911–2). The spirulæ of the former do not, however, attain such a large size as those of the latter and their modal value is lower. It is possible that this discrepancy is explained by a difference in the size of the Dingle anemones from which the cells were taken compared with those studied from the other localities, since smaller spirulæ (**16**) and smaller penicilli (see Table I) occur in the young than in the adults of the typical *M. senile.* The anemones from which the data were obtained for Figures 4 and 5 were all small, but their shape is so variable that only their approximate size can be measured. The penicilli do not show any appreciable difference in either their range in size or their modal value (see Fig. 5), which suggests that possibly some other factor is contributory to the smaller size of the spirulæ. Maybe it varies slightly in different localities, possibly with salinity and perhaps in the case of the Dingle anemone, the dwarfing of the body is reflected to some degree in the individual cells.

Three very large specimens, a brown one from Plymouth and an orange and a white one from Port Erin, all showed a relative scarcity of penicilli compared with their numbers in the small individuals. After several days' continued search only six were found in the Plymouth anemone. They were similar in size and shape to those of the scapus ectoderm but their capsules were only approximately half the length of the penicillus

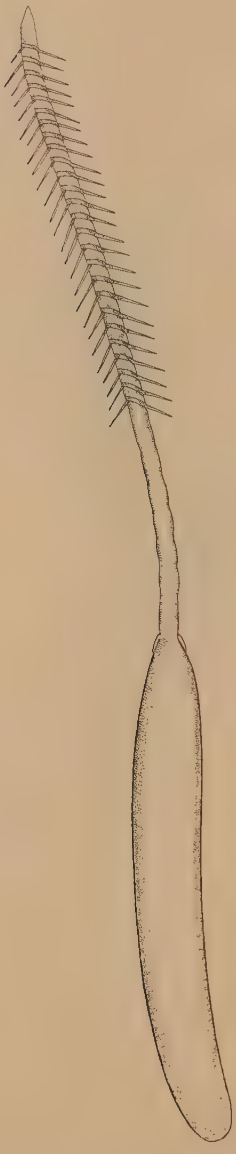

FIG. 2.—A penicillus from an acontium of a typical *M. senile* × 1800.

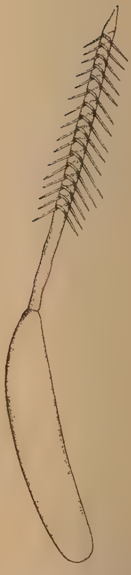

FIG. 3.—A penicillus from the ectoderm of a typical *M. senile* × 1600.

capsules found in the acontia of the other small individuals which had been examined. Their scarcity, together with their resemblance to those of the scapus, led one to conclude that penicilli were absent from the acontia, but that a few stray cells, probably from the ectoderm, had adhered to the acontia after or during their extrusion. Penicilli were also absent from the acontia of the white specimen from Port Erin, but a few of the usual type and size were found in the orange-coloured one (see Table I). The acontia of eight additional Plymouth specimens with a column height ranging from 3·5–6·5 cm. showed the same scarcity of penicilli.

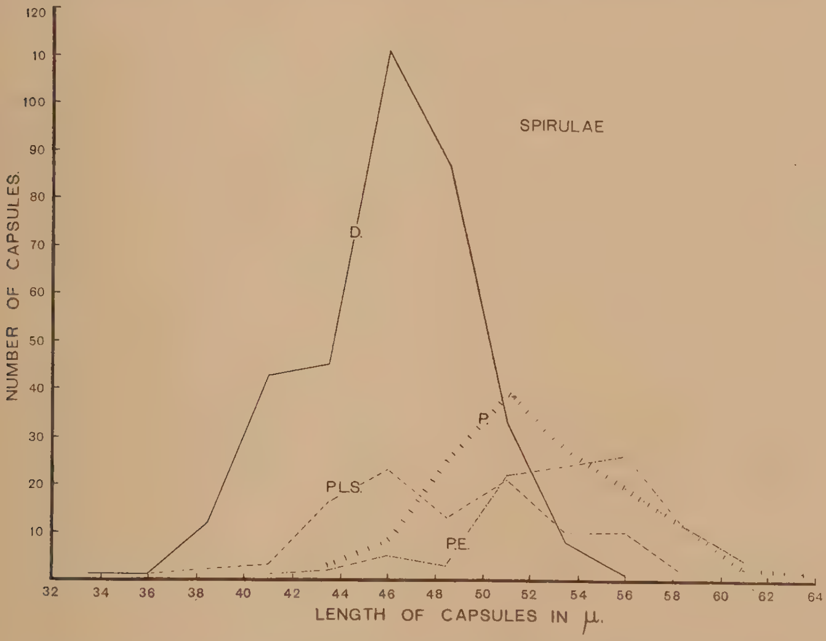

FIG. 4.—Graphs showing the variation in length of the spirula capsules, exploded and measured to the nearest 0·5μ, from the acontia of the Dingle anemone and *M. senile* from the Princes Landing Stage (Liverpool), Plymouth and Port Erin.

D.	340 cells from the Dingle specimens in Table I.
P.L.S.	100 cells from the Princes Landing Stage specimens in Table I.
P.	132 cells from the small Plymouth specimens in Table I.
P.E.	100 cells from the small Port Erin specimens in Table I.

The particular function of the penicilli is unknown and the reduction in their number in large specimens is as yet inexplicable. In some Cœlenterates (**18**), the developing nematocysts are migratory. It is possible they are so in *M. senile* and that there is a difference between their migratory powers in the young and the adults. One would expect to find wandering cells in the young rather than in the old individuals.

A comparative study of the types of cnidæ occurring in the ectoderm of the scapus has shown that these cells also are structurally similar and comparable in size in the Dingle anemone and *M. senile* (see Table I). Both spirulæ and penicilli are present. The spirula capsules are smaller than those found in the acontia. The spiral is uniform in width, limited to a short distance at the base of the thread and has three to four turns, whereas the spiral of the acontia spirulæ is much more extensive with about twenty turns and considerably expanded towards its distal end (**16**, Fig. 1). There are at least two distinct kinds of penicilli, a small one with a rather globular capsule and a distinct wisp-like terminal thread and a larger variety (Fig. 3) similar to, but smaller than those found in the acontia and with an elongated oval capsule. The latter are very much

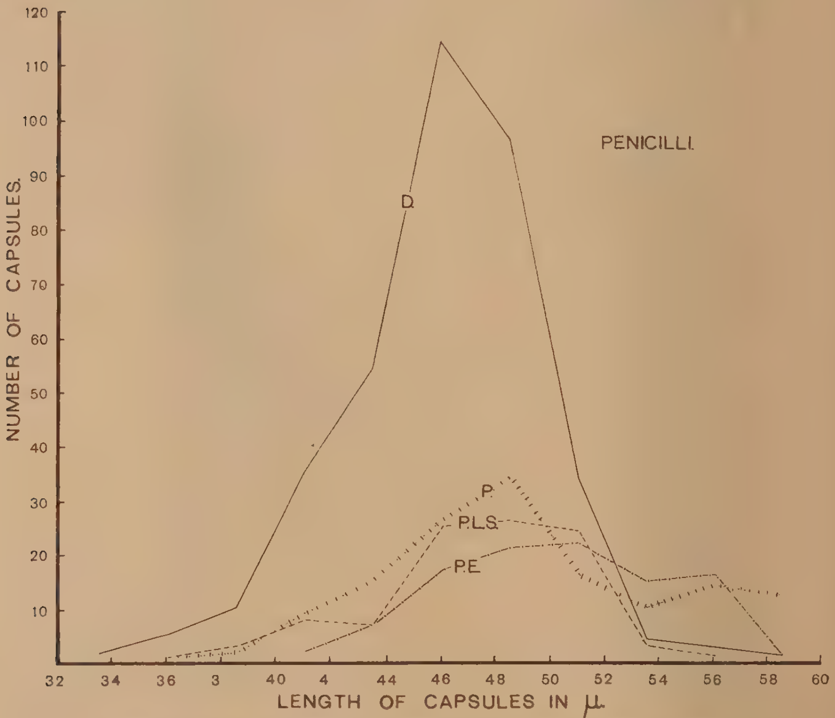

Fig. 5.—Graphs showing the variation in length of the penicillus capsules, exploded and measured to the nearest 0·5μ, from the acontia of the Dingle anemone and *M. senile* from the Princes Landing Stage (Liverpool), Plymouth and Port Erin. The cells were taken from the same anemones as gave the data for Fig. 4.

D.	354 cells from the Dingle specimens.
P.L.S.	100 cells from the Princes Landing Stage specimens.
P.	140 cells from the Plymouth specimens.
P.E.	101 cells from the Port Erin specimens.

TABLE I.

MEASUREMENTS OF THE SPIRULA (SP.) AND THE PENICILLUS CAPSULES (PEN.) OCCURRING IN THE ACONTIA AND THE SCAPUS ECTODERM OF THE DINGLE ANEMONE AND *M. senile*.

(The measurements were made on living cells exploded in sea-water and unstained except the ectoderm cells which were stained with 1% acid fuchsin.)

Locality.	No.** of specimens examined.	Approximate diameter in cm.		No. of cells measured.			Range in size of the cells in μ.	Average size of the cells in μ.
		Base	Disc					
Dingle	5	1·2	1	Ectoderm	Pen.	95	11–20·5 × 3–4·5	16·2 × 3·6
				Acontia	Sp.	100	38·5–55·5 × 3–4·5	47·9 × 3·6
				,,	Pen.	100	34·5–54 × 3·5–6	47·1 × 5
	8 (1 g.)	0·6	0·8	Acontia	Sp.	156	33–50·5 × 3–4·5	44·6 × 3·6
				,,	Pen.	160	32–51 × 3–6	44·9 × 4·9
	4	1	1	Acontia	Sp.	80	38 -53·5	46·8
				,,	Pen.	80	39–58	47·1
	1		0·5	Ectoderm	Sp.	20	9·5–13 × 1·5–3·5	11·3 × 2·4
				,,	Pen.	21	13–19·5 × 3–4·5	16·3 × 3·4
	1		1	Ectoderm	Sp.	20	10–15 × 2·5–3·5	12·3 × 2·8
				,,	Pen.	20	16–20 × 3·5–4	18 × 3·7
				Ectoderm	Sp.	20*	9·5–13·5 × 2–3·5	12·5 × 2·7
				,,	Pen.	20*	13–21 × 3·5–5·5	18·8 × 4·3
Princes Landing Stage	5 (br. and p.)	1·4	1·1	Acontia	Sp.	100	35·5–59 × 3–5·5	47 × 3·8
				,,	Pen.	94	36·5–53 × 4–6·5	47·3 × 5·3
Plymouth	1† (br).		12·5	Ectoderm	Sp.	20	11–19·5 × 1·5–4	15·9 × 2·6
				,,	Pen.	21	20–27 × 2·5–4·5	24·4 × 3·4
				Acontia	Sp.	23	57–69·5 × 3–4·5	63·4 × 3·4
				,,	Pen.	0	Absent	
	1 (n.r.)		0·4	Ectoderm	Sp.	12	9–13·5 × 1·5–3	11·7 × 2·2
				,,	Pen.	16	13·5–18·5 × 3–4	16 × 3·4
				Acontia	Sp.	13	42–53 × 3–4	48 × 3·6
				,,	Pen.	21	40–48 × 4–5·5	43·4 × 4·8
	3	0·5	0·8	Ectoderm	Pen.	31	10·5–25·5 × 3–5	17·2 × 3·5
				Acontia	Sp.	60	44–59 × 3–4·5	51·3 × 3·8
				,,	Pen.	60	42–59 × 4–6	49·9 × 4·9
	4 (br. p. w. and n.r.)	0·5	0·7	Acontia	Sp.	59	45·5–64·5 × 3–5	53·6 × 3·7
				,,	Pen.	73	38–59·5 × 4–6·5	48·3 × 5
	1† (n.r.)		2·7	Ectoderm	Sp.	20	9·5–16 × 1·5–3	14·1 × 2·5
				,,	Pen.	16	16–22 × 3–4	20 × 3·4
Port Erin	5 (o. and w.)	1·4	1·4	Acontia	Sp.	100	35–62 × 2·5–4·5	53·3 × 3·5
				,,	Pen.	101	41–57·5 × 3–6·5	50·1 × 4·8
	1† (o.)		10	Acontia	Pen.	16	53–62 × 4·5–6	57·3 × 5·2

* These cells were unexploded and unstained.

† The stinging cells from these specimens are not used in Figs. 4 and 5.

** Colour pink, unless noted as :—
br. = brown, g. = grey, o. = orange, w. = white, n.r. = not recorded.

more abundant than the former; they sometimes show a terminal thread. All the measurements refer to the larger kind. Their size varies but little between different individuals of about the same size, but like the stinging cells of the acontia they are slightly larger in old specimens than in young ones.

To summarise the observations on the nematocysts one may say:—

i. the spirulæ and penicilli from the acontia and the scapus ectoderm of the Dingle anemone are identical in form and comparable in size with those found in *M. senile.*

ii. both spirulæ and penicilli are present in abundance in the acontia of typical small *M. senile* from various localities, but they are sparse and sometimes absent from large and medium-sized individuals.

iii. the acontia of the largest and the smallest specimens of the Dingle anemone contain an abundance of spirulæ and penicilli; some of the anemones were sexually mature.

The Dingle Anemone as a New Species or a Variety of *M. senile.*

The close correspondence between the habits, the methods of reproduction, the anatomy, the types and sizes of the stinging cells from the ectoderm and the acontia, as noted in the foregoing sections, gives quite sufficient evidence for regarding the Dingle anemone as *M. senile.* It nevertheless exhibits certain features which at present justify its recognition as a dwarf variety. The small size of all the individuals composing the colony and their attainment of sexual maturity while small support this suggestion. The fertile specimens also exhibit the following characters of the young of the ordinary type; the general appearance of their tentacles, the abundance of penicilli in their acontia and the absence of clear disc lobes. Much of the interest of these characters would be lost should further researches prove that the typical form is sexually mature at a smaller size than is thought at present.

Gosse (3) observed young specimens of Metridium between the tide-marks and suggested that with advancing age they move offshore to deeper waters. Perhaps the Dingle anemones migrate, but actual proof of this habit is difficult to ascertain. Their dwarf form is possibly associated with the separate or combined effects of the following factors; their intertidal position, the low salinity and the pollution of the water.

One small fertile specimen was sent to the Laboratory, Plymouth, where it was fed with plankton. It did not show any appreciable change in size after living there for seven months. A subject for further experiment is to determine whether the Dingle anemones are permanently dwarfed, or whether if transferred to other more favourable environments they would grow to the average size and develop all the characters of the type species.

THE SYSTEMATIC POSITION OF THE GENUS METRIDIUM.

Some of the principal changes in the systematic position of Metridium are shown below :—

Fam. SAGARTIADÆ Gosse (**3**, 1860), including the genera Actinoloba (=Metridium) Sagartia, Phellia, Adamsia, Gregoria, and Discosoma.
Fam. SAGARTIDÆ (Hertwig, 1882).
Sub. fam. Metridinæ, Carlgren (**10**, 1893), including the genera Metridium, Adamsia, Aiptasia, Stelidiactis, and Calliactis.
Fam. METRIDIIDÆ Stephenson (**15**, 1920), including the genera Metridium, Calliactis, Adamsia, Aiptasia, Aiptasiomorpha, Heteractis, and Bartholomea.
Fam. METRIDIIDÆ Stephenson (**16**, 1929), including the genera Metridium, Calliactis, Adamsia, Hormathia, Actinauge, Paraphellia, Leptoteichus, Chondrodactis, etc. (and the remaining genera included in the Metridiidæ and Chondractiniidæ **15**, 1920, with the Aiptasiids and Sagartiomorphe removed).

In 1860 it was classed with the Sagartias in the family Sagartiadæ (**3**). Many years afterwards Carlgren (**10**) placed it in his new sub-family, the Metridinæ. Stephenson (**15**) renamed the sub-family Metridinæ the Metridiidæ, and raised it to the rank of a full family on a level with the Sagartiidæ. Later, as the result of much work on the nematocysts of anemones with acontia, he revised the members and the characters of these two families (**16**, 1929), and in addition to the characters given in his earlier classification he provisionally distinguished the Sagartiidæ as forms with an abundance of spirulæ and penicilli in the acontia and the Metridiidæ as forms possessing spirulæ only. The resemblances and differences between the Sagartiidæ and the Metridiidæ (**16**) strongly suggest a reconsideration of the systematic position of the genus Metridium, as both spirulæ and penicilli have recently been found in the acontia of the young of the typical *M. senile.*

The general systematic value of the presence or absence of cinclides and the position of the gonads has already been queried (**12**). If the type of stinging cell found in the acontia is to remain a family character, then Metridium must be removed from the family Metridiidæ provided that further researches on *young* and *adult* specimens of Adamsia, Calliactis and the other genera included in the family prove the absence of penicilli from their acontia. There seem to be only two alternative positions for it, either it must once more be classed with the Sagartias in the Sagartiidæ or else it must be placed in a family by itself as recently suggested by Carlgren (**17**, 1933). There are points in favour of both these suggestions.

Since the discovery of both spirulæ and penicilli in the acontia of *M. senile* and the Dingle variety, there exists no constant difference between the Sagartiidæ and the Metridiidæ. This is the principal evidence in favour of placing Metridium with the Sagartias. Such a grouping would probably be quite satisfactory for the young individuals of *M. senile*, but the presence of a distinct collar and the possible absence of penicilli from the acontia of the adults directly oppose this classification. It is noteworthy that one of the family characters quoted in the past for the Sagartiadæ (**3**), which contained the genus Metridium, is the presence in the acontia of cnidæ with a short densely armed wire. They are obviously penicilli.

If the genus is placed in a family by itself the characters of such a family cannot be anything but indefinite because certain of the features exhibited by the young and adults are different, moreover, the form of the body, the number of perfect mesenteries and the position of the gonads are variable characters. There is, however, a more marked tendency towards the sterility of the primary mesenteries and to hexamerism in the genus Metridium than in the Sagartias.

A consideration of these characters and the above-mentioned objections to placing the genus with the Sagartiidæ, together with the further evidence of the presence of penicilli in the acontia of both *M. senile* var. *dianthus* and the Dingle variety, favours Carlgren's suggestion of restricting the Metridiidæ to the genus Metridium. The remaining genera of the present Metridiidæ may then be referred to the Chondractiniidæ (now the Hormathiidæ, **19**), as suggested by Professor Stephenson (letter to the author, 4. 4. 34). The evidence obtained from the stinging cells of the acontia and the general trend of certain characters of the genus along a path distinct from the Sagartias support these suggestions. The types of stinging cells in the acontia would not alone be a useful diagnostic character for the revised Metridiidæ, since the number of types present varies with the age of the individual. In conjunction, however, with the unique form of the spirulæ from the acontia, and the characters already described for the genus (**15**), one would have ample features on which to base a description of a family which contained the genus Metridium as its sole representative.

Unfortunately, living specimens of *M. marginatum*, Milne-Edwards, *M. fimbriatum*, Verrill, and *M. senile* var. *pallidum* (Holdsworth) have not been available for an investigation of their stinging cells, but Carlgren (**17**, 1933) has now recorded the presence of penicilli in one small

Metridium sp. and one large specimen of *M. fimbriatum.* It is highly probable therefore that all these forms would fit in with the revised Metridiidæ since the var. *pallidum* is not very different from the ordinary type and, as previously noted, certain authors regard the American species and the European *M. senile* as synonymous.

The following conclusion may be drawn from the foregoing discussion. The variation which is met with in the genus Metridium and the difficulties which present themselves in connexion with its systematic position show that the genus is transitional between the Sagartiidæ and the Metridiidæ as defined in 1929. Its affinities with the Aiptasiidæ have also been mentioned by Carlgren (**17**). Some specimens of Metridium exhibit characters which suggest a trend towards the Sagartias, but others possess features which are different from those of this family, namely, hexamerism and the sterility of the perfect mesenteries. An intensive study, nevertheless, shows that they are all referable to the one genus. The Sagartian trend of the genus is further emphasised by certain characters of the Dingle anemone. In many ways it is true to type, but in addition to the frequent occurrence of more than six pairs of perfect mesenteries, both young and adults possess an abundance of penicilli in their acontia. The latter is a feature of the Sagartias and one which at present distinguishes the adults of the Dingle form from the adults of the typical *M. senile.* The asexually produced polyps of the latter often show the Sagartian feature of more than six pairs of perfect mesenteries, some of which may bear gonads. The deviation from hexamerism is not entirely due to the mode of reproduction (see p. 906) and moreover, other anemones, e.g. Aiptasia, which reproduce by basal laceration, always give rise to daughter polyps which are diglyphic and hexamerous irrespective of the size and constitution of the original fragment (**4**). In the latter species hexamerism seems to be a stable character, whereas in Metridium the inherent tendencies to this primitive condition are not so pronounced.

The presence of acontial penicilli appears to be a constant character of the Dingle anemone and should future investigation show that irregular polyps normally arise by sexual reproduction then such a form of Metridium would be almost as near to the genus Sagartia as to the genus Metridium; the presence of a distinct collar in the latter does, however, distinguish the two genera. A large amount of experimental work involving the rearing of egg embryos would be necessary to prove this point. Until more is known about the morphology of egg embryos the true state of affairs within the genus cannot be estimated.

SUMMARY.

1. A special study has been made of a small Metridium-like anemone found at Dingle, Liverpool, in comparison with the typical form of *Metridium senile* (L.) var. *dianthus* (Ellis).

2. Penicilli, formerly believed to be absent from the acontia of typical *M. senile*, have been discovered in abundance in the young, but rarely in the adults. In young and sexually mature specimens of the Dingle anemone they are also abundant.

3. There is close agreement between the anatomy of the Dingle form and the typical *M. senile.*

4. A considerable amount of variation occurs in the Dingle anemone, as in *M. senile* var. *dianthus* and *M. marginatum*, Milne-Edwards.

5. The resemblances and differences between the Dingle form and *M. senile* indicate that the former is a dwarf variety of the latter.

6. The discovery of an abundance of penicilli in the acontia of young typical *M. senile* and mature specimens of the Dingle variety, in conjunction with the great amount of variation in the genus Metridium, suggests that a reconsideration of the systematic position of the genus is necessary and would justify either the restriction of the family Metridiidæ to the single genus Metridium, or else the fusion of the Metridiidæ with the Sagartiidæ. The sum of the evidence appears to lie in favour of placing the genus in a family by itself.

ACKNOWLEDGEMENTS.

I am much indebted to both Professor Orton and Professor Stephenson for their kindly helpful criticism and particularly to Professor Stephenson for the manuscript of the chapter on Metridium intended for the forthcoming second volume of his monograph on the British anemones, and for his very generous help with the discussion on the systematic position. Unfortunately I have been unable to quote all his suggestions as they arrived after the paper had gone to the press.

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The Flow of Water Past the Seven Stones Lightvessel.

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INTRODUCTORY REMARKS—WITH BRIEF REFERENCE TO RELEVANT EXISTING INFORMATION.

THE purpose of this paper is to place on record the results of a series of current measurements carried out from the Seven Stones Lightvessel in August and September, 1933.

The observations are believed to be the first set of direct current measurements of any duration made in the area. The instrument employed was a Drift Indicator such as has long been in constant use at the Varne Lightvessel, and of which a full description is readily available in the popular pamphlet which appeared as No. 17 of the Ministry's series of " Fisheries Notices."

Details as to the duration and continuity of the observations to be dealt with can be gleaned from the table given below.

It may be recalled that what one learns from the employment of the instrument in question, is the residual current—or what Doodson has called the average constant current.

It is hoped before long to carry out from the Seven Stones Lightship, precisely similar continuous current observations to those which have been in train for more than eight years from the Varne Lightvessel, and the investigation below dealt with was in the nature of a preliminary experiment.

Thanks are due to the Trinity House for permission to make the observations from their lightship; to their District Superintendent concerned (Captain R. W. V. Plimsaul), to the officers of their steamer S.V. *Mermaid* (Messrs. J. C. McCarthy and C. E. K. Carpenter), and in particular to the Master of the lightvessel (Mr. T. Boyd) who, besides making the observations, logged the relevant wind and sea particulars.

The Seven Stones Lightship is moored at 50° 03′ N.–6° 04′ W. in 39 fathoms of water; its position therefore is about 14 miles due west of Land's End.

The observations were made (as at the Varne) at the nominal depth of six fathoms.

It would be of considerable interest fully to relate the results which we shall present below to prevailing ideas concerning the nature of the water movements in the Land's End–Scillies passage, to what is known of the circulation at large off the mouth of the Channel and the entrance to the Irish Sea, and also to the Rennell Current question.

Exigencies of space preclude more than a few brief remarks in these connections. The reader who is acquainted with the relevant literature will know that any adequate account presenting citations from the publications of Matthews, Harvey, Lumby, Gehrke, and others, would convey the impression that the most usual direction of water flow through the passage is towards the northern half of the compass.

Admiralty tidal stream observations relating to the position of the lightvessel itself, and to another position about 16½ miles away towards S. 30° E., could be shown to imply the existence of a set towards the S.E. quadrant, but it is not at all easy to decide just what degree of reliance can be placed upon indications of overall water flow derived from vector-averaging such tidal stream data.

Examination of the records sent in to the writer when the month's observing on the Seven Stones Lightvessel was finished, revealed that there had been a flow of water towards the S.E. quadrant at the depth of six fathoms—this as the resultant for the entire period of 28 days.

In a well-known paper (**1**) setting forth the results of a hydrodynamical study of the water movements in the area here concerned, Harvey deduced the existence of a north-going difference in velocity between the surface water and the layer at 60-metres depth, amounting to 1½ miles a day—this between Land's End and the Scillies at the end of June, 1924. He declares elsewhere, that " there can be little doubt of the existence of such a residual current superimposed on the tidal streaming, and carrying water northward into the mouth of the Bristol Channel—variable in velocity and perhaps intermittent."

Harvey's deductions from his hydrodynamical study accorded well with those earlier made by Matthews from the consideration of temperature and salinity distribution, and upon which he based his conclusions as to the circulation in the area. His (Harvey's) results do not tell us what was the overall movement of the entire water column ; his values would have to be compounded with the vectors representing the movements of the water below 60 metres before we could learn that.

Harvey's stated conclusion for the Land's End–Scillies passage was that the surface water had its own proper movement of 1½ miles a day towards N.N.E. over the water below 60 metres—this direction of movement being declared to be suggested by the trend of the pressure contours on his chart. A glance at the latter, however, makes one suppose that " N.N.E." is a misprint for " N.N.W."

As regards the water movements in the Irish Sea at large, it is well known that there is a residual streaming towards the north, and that it has been inferred from purely physical data that the whole body of water in the Irish Sea is changed every year, and that it passes to the north between Ireland and Scotland.

When one is considering the water movements off Land's End, one's thoughts readily turn to the Rennell Current, for if a north-going flow of water across the mouth of the Channel were the most usual state of affairs, one might reasonably expect a northerly set off Land's End to be the rule. If, however, it could be shown that the direction of water flow through the Scillies-Land's End passage is most usually southerly, there would be reason to expect that the Rennell Current can be nothing more than an occasional phenomenon, and some measure of justification for supposing Krümmel to be right when he declares that "Nach alledem wäre es endlich an der Zeit, den Rennellstrom von den Karten zu tilgen."

Events *in re* currents off Land's End can hardly fail to be linked up with the water movements to the south, and the driving force of the Rennell Current merits a few words. Tait has recently found that with certain pooling-up conditions in the Moray Firth due to an unusually strong inset from seawards, an escape-current can be generated, which, trending north, can head across the ocean passage north of Scotland and cut off the usual inflow.

Since the Rennell Current is held to be born of similar effects in the Bay of Biscay, may not it too be a similarly occasional phenomenon ?

If it is, then we ought not to be unduly surprised if we find reason to suppose that there is most usually a S.E.-going flow through the Scillies–Land's End passage.

If the remarks made above, in conjunction with the results to be set out below, lead to further investigations designed to ascertain the most usual state of affairs, our chief aim in writing this paper will have been achieved.

The Records Obtained.

Below we tabulate the results of the 28 days' observations at the Seven Stones Lightvessel.

Tidal Streams.

Our first comment on the table can well refer to the tidal streams, since comparison between our data and those available in the Admiralty Manual (**2**, page 40) besides being of interest, can be very easily made.

We find that the total mileage run per tidal period of the streams in all the directions concerned can, according to the showing of our Drift Indicator, be taken as 7·3. This value can be regarded as a representative average.

RESIDUAL CURRENTS AND WINDS AT THE SEVEN STONES LIGHTVESSEL DURING A 28-DAY PERIOD IN AUGUST–SEPTEMBER, 1933.

Serial Reference Number of the Record.	Duration of the Observation in Lunar Days.	Dates and Terminal Hours of the Observation.	Residual Current ; Sea Miles per Lunar Day towards a true Direction.		Tota Mileage of To-and-fro Water Movements.	The same per Tidal Period.	Moon Phases.	Residual Wind during the time of the Observation (Based on Eight Estimates per Day made aboard) in Miles per Hour from a true Direction.		Angle in degrees between Residual Current and Residual Wind directions : "r" denotes current set to right of wind, and "l" current set to left of it.
1	1	0910 (17.8.33)–1000 (18.8.33)	6·5	S. 34° E.	12·7	6·4		14·6	S. 50° W.	96 r.
2	1	1010 (18.8.33)–1100 (19.8.33)	3·6	S. 11° E.	11·7	5·8		6·5	S. 49° W.	120 r.
3	1	1110 (19.8.33)–1200 (20.8.33)	4·9	due S.	14·8	7·4		14·0	N. 80° W.	80 r.
4	1	1210 (20.8.33)–1300 (21.8.33)	11·8	S. 21° E.	19·2	9·6	New on 21st	20·6	N. 70° W.	49 r.
5	1	1310 (21.8.33)–1400 (22.8.33)	12·4	S. 1° W.	22·7	11·4		15·2	N. 77° W.	78 r.
6	1	1410 (22.8.33)–1500 (23.8.33)	10·9	S. 2° E.	23·6	11·8		23·0	N. 68° W.	66 r.
7	1	1510 (23.8.33)–1600 (24.8.33)	9·1	due S.	20·5	10·2		6·2	N. 89° W.	89 r.
8	1	1610 (24.8.33)–1700 (25.8.33)	3·3	S. 20° W.	19·3	9·6		6·7	S. 43° E.	117 l.
9	1	1710 (25.8.33)–1800 (26.8.33)	3·7	N. 77° E.	14·6	7·3		5·7	S. 66° E.	143 r.
10	1	1810 (26.8.33)–1900 (27.8.33)	4·7	N. 32° E.	13·5	6·8		5·2	S. 24° E.	56 r.
11	1	1910 (27.8.33)–2000 (28.8.33)	2·8	N. 64° E.	13·3	6·6	First Quarter on 28th	9·4	S. 31° W.	33 r.
12	1	2010 (28.8.33)–2100 (29.8.33)	2·9	S. 79° E.	8·2	4·1		5·3	S. 70° W.	31 r.
13	3	2110 (29.8.33)–2340 (1.9.33)	2·8	N. 78° E.	29·8	5·0		6·5	N. 57° W.	45 l.
14	3	2400 (1.9.33)–0230 (5.9.33)	3·4	S. 68° E.	60·2	10·0	Full on 4th	4·5	N. 56° E.	124 l.
15	3	0240 (5.9.33)–0510 (8.9.33)	2·0	N. 4° E.	61·2	10·2		8·1	N. 77° E.	107 r.
16	3	0525 (8.9.33)–0755 (11.9.33)	1·5	N. 2° W.	32·0	5·3	Last Quarter on 11th	12·9	N. 65° E.	113 r.
17	2	0805 (11.9.33)–0945 (13.9.33)	6·4	N. 36° W.	20·9	5·2		5·8	N. 64° E.	80 r.
18	2	0955 (13.9.33)–1145 (15.9.33)	3·2	S.61° W.	11·8	3·0		4·7	N. 41° E.	20 r.
All	28	0910 (17.8.33)–1145 (15.9.33)	1·9	S. 20° E.	410·0	7·3		1·6	N. 27° W.	77 r.* 7 r.

* This average does not take account of the three "l's."

Now the Admiralty tidal stream data for the position of the Seven Stones Lightship show that the total to-and-fro streamings per tidal period amount to 10·1 miles—this being at the time of spring tides. Assuming, as seems from Warburg's manual (**3**, page 73) to be justifiable, that the average rate of the streams can be taken as three-quarters of their spring rate, we obtain the value 7·5 to compare with ours of 7·3. This degree of accordance is very satisfactory indeed.

Our Drift Indicator data show that the spring-stream speed as given in the Admiralty Manual must be exceeded on occasion, and that the neap-stream speed can be less on occasion than that inferable (5·0 miles per tidal period) from the Admiralty data.

We do not propose to set down here any further details concerning the tidal streams, save to say that the Drift Indicator records show the dominant opposing directions to be about S. by W. and N. by E.

Residual Currents: Inter-relationship Between Wind and Water Movements.

Let us next turn to consider the residual current, which is our main concern. We see that over the whole period of 28 days there was an overall set towards S. 20° E. true and of amount 1·9 miles per day. This is the quantity in which we are most interested, for, although it is an average smoothing out residual currents of varying strengths and directions, it is the quantity with which anyone making deductions from salinity distribution would unconsciously be concerned. This is so because salinity distribution would be conditioned by the integrated effects of varying sets over a considerable period.

It is seen that there was during the entire period of 28 days, a residuum of wind travelling (within a little) in the same direction as that towards which the overall transport of water at 6 fathoms depth was effected, and it is of considerable interest to note the relative magnitudes of the residual wind and water speeds concerned.

The water speed is just a little less than 5 per cent of the wind speed, and, since residual wind and residual current are here in practically the same direction, and since they refer to a period of time long enough to be significant, we can compare the result just obtained with a similar one found earlier.

The present writer in 1930 (**4**) advanced a relationship between speed of surface drift-bottle travel up-Channel and speed of wind. In that case the effective wind in an up-Channel direction was in question, and both bottle and air travel related to considerable periods of time. The corresponding relationship was :—

Bottle travel=1/18th wind travel.

The fraction 1/18th being 5·5 per cent, the two values tally very well—particularly as the lesser one has to do with a water layer so much below the surface as 6 fathoms. Statements could be quoted to the effect that in high latitudes the rate of water drift communicated is about 2 per cent of the velocity of the wind—and 4 per cent in low latitudes. Such statements would not necessarily be in conflict with our findings, for a higher percentage would be expected to apply where residual winds and residual currents representative of considerable periods of time are in question. We here regard our numerical relationship as nothing more than an empirical one good for the area concerned. It may have some potential usefulness, though we shall greatly hesitate to invest it with any real importance until further investigations have been made to see whether such a value emerges again. Such hesitancy is very understandable when it is remembered that we have been dealing with the water movements at 6 fathoms depth. Our reason for relating the two quantities: wind speed and water flow, is the realisation that the individual records evince a large measure of change on the part of the currents with the wind—which fact leads us to suppose there to be some inter-relationship. There are certain features of the entries in our table which suggest that we are far from entitled to assume that, if we repeated the observations many times for a like term, we should find that residual wind and residual current would customarily be directed so nearly in the same direction. A mere glance at the table shows that for a short period of time, residual current at 6 fathoms depth and residual wind can be at a large angle with each other.

ANGLE BETWEEN CURRENT AND WIND.

Inspection of the current and wind data relating to the individual records reveals much of interest. It is to be remarked that in fifteen records (i.e. in all but three) the current set at 6 fathoms depth was directed to the right of the wind. In the three cases (records Nos. 8, 13, and 14), where the current was directed to the left of the residual wind, there had been an abrupt change of wind.

A very interesting feature indeed is that the current was directed to the right of the wind when the latter was from any one of the four quadrants, there having been a current set to the right of the wind for :—

4 cases of wind from the S.W. quadrant.
5 cases of wind from the N.W. quadrant.
4 cases of wind from the N.E. quadrant.
2 cases of wind from the S.E. quadrant.

Much space would be needed to give an adequate analysis of the data in this connection.

Clearly from what we have seen (*in re* records No. 8, 13, and 14) there must elapse some time before, after a change of wind, the current can take up the direction which would accord with the new wind direction. The angle between wind and current at 6 fathoms depth may well be a more or less constant quantity for this area where a wind of persistent direction and long duration is concerned; this we do not know, but in the near future shall endeavour to ascertain. Since the observations here being considered were made at a time when very changeable wind conditions were encountered (a fact in no way to be regretted since we have found what we have found about the relation of current direction to wind direction for winds from all four quarters) it results that the angles between current and wind vary greatly—from about 140 degees down to 20 degrees.

It is to this substantial variation that we must attribute the fact that the residual current and residual wind for the entire period of 28 days are directed towards the same point of the compass—within a little. The fact that the winds varied so much in strength must have meant that the current would swing into a new direction with change of wind less quickly in some cases than in others, and this would account for some measure of the variation in the value of the angle, and would add to the likelihood that it would be smoothed out of existence in the process of averaging over a "longish" period.

As it is, the residual current for the entire period of 28 days shows some small amount of "right deviation" which the compounding of such variant vectors has not entirely smoothed out.

It is to be expected that, after many months of observation on the Seven Stones Lightship, long period means would display the existence of an angle between current and wind. What the value of that angle would be we cannot presume to guess, but are surely entitled to assume that the current would set to the right of the wind.

The angle made to the right of the residual wind by the residual current at 6 fathoms depth can of course be easily worked out as an average for the 15 individual records above tabulated. The resulting mean value is about 80 degrees.

In view of the variation displayed, we may not accept this magnitude too confidently, but one thing we can do which seems promising: we can pay attention to records Nos. 3 to 7 which relate to a period of persistent strong winds from the N.W. quadrant, and can there see that the "right deviation" varies from 49 to 89 degrees.

If the value of 80 degrees were considered to be acceptably established, we should feel disposed to assume that the layer of water at 6 fathoms depth was little above that containing the centre-of-mass of the entire body of water which the wind was able to set in motion.

The prospect of evaluating the separation angle in the future is very attractive ; for the present we are interested to see that in only three out of the fifteen records showing right deviation was the angle less than the 45 degrees which needs no comment.

No further remarks are called for on this matter since it will receive detailed attention after more observations with the Drift Indicator from the Seven Stones Lightship have been made.

Generalisation from the Present Findings as to the Most Usual Direction of Water Flow through the Land's End–Scillies Passage.

It can be seen from our table that, although the overall set during the entire 28-day period was towards the S.E. quadrant, yet actually there was just as often a set towards the north of the E.-W. line as towards the south of it —14 days in each case. There was more often a set towards the east of the N.-S. line than towards the west of it—17 days against 9. In so far as our results, relating as they do to a time of dominant N.W.'ly winds, might be considered not representative of the most usual state of affairs, we should remark as follows :—

The most usual direction of wind being from the S.W. quadrant, we should, judging from what we have seen as to the relation between wind and current directions, expect the set to be most frequently directed towards the S.E. quadrant, and not (as seems to be the prevailing opinion) towards a northerly point.* We should expect a persistent set towards the quadrant between N.E. and N.W. only during months characterised by wind conditions from S.E. to N.E. respectively.

These findings and expectations would lead us to doubt the existence of the Rennell Current except as an intermittent phenomenon, that is to say, we should expect there to be a north-going set off the Channel mouth much less frequently than would entitle us to perpetuate the Rennell Current.

It seems abundantly clear that many more direct current-meter observations are needed before we can hold really definite ideas as to the most usual state of affairs concerning the currents off Land's End.

Varne Current and Drift-bottle Particulars.

During the first six days of the Seven Stones observations above dealt with, the Dover Straits current was heading strongly and boldly (i.e. with a fair amount of east in it) into the North Sea. Thereafter, up to

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* In this connection it is of real interest to recall the implications of the Admiralty tidal stream data briefly referred to above. As we now see, the S.E.—going set which they implied may well be—as Harvey (5, p. 67) supposed possible—a wind drift, but a wind drift induced by S.W.'ly winds.

September 7th, conditions of "hold-up" of the Varne current prevailed. After that the Dover Straits current was strongly reversed—this at the time when the Seven Stones current was flowing towards north and west of north.

Ten surface drift-bottles are put out each Monday from the Seven Stones Lightship. Four liberations were made during the time of the Drift Indicator observations, but as yet only one bottle (set out on September 11th) has been recovered. This was found 121 days afterwards (on January 10th, 1934) in statistical sub-rectangle UU 4g., that is on the west coast of Ireland in latitude 52° 30′ N. approximately.

Such a recovery position is very unusual, though one or two other bottles have been recovered on the west Irish coast. The bottle would have commenced its journey at the time of our record No. 17 (see Table above) and would have got a good start towards the N.W.

SUMMARY.

A brief reference to the state of opinion concerning the water movements off S.W. England is made. Then a series of Drift Indicator records relating to 28 days of observation at 6 fathoms depth from the Seven Stones Lightvessel is presented and discussed. An overall flow of water towards the S.E. quadrant and of speed approaching 2 miles per day characterised the entire period. The residual current as worked out for the individual records, displayed considerable variation in speed and direction —setting as frequently towards the northern half of the compass as towards the southern, but more frequently towards the eastern half than towards the western half. There were pronounced changes in the wind speed and direction, and it appears as though the wind can drive the water at 6 fathoms depth towards a point to the right of its own direction, no matter from which of the four quadrants it blows.

There is good reason to suppose that the angle between the 6 fathom current direction and that of the wind in this area would almost always be greater than 45 degrees. Observations occupying 21 days yielded an average value approaching 80 degrees.

During the entire period of 28 days, an overall transport of water towards the same direction (within a few degrees) as the residual wind proper to the whole period was effected at 6 fathoms depth—the speed of the water flow being about 5 per cent of that of the wind. This result accords very closely with an earlier relationship worked out between drift-bottle travel up-Channel and wind flow up-Channel. Since the most usual direction of wind is S.W.'ly, the findings regarding the angle between wind and current are held to justify the expression of opinion that the most usual direction of water flow through the Land's End–Scillies passage

will be towards the S.E. quadrant. This opinion is in conflict with deductions which have been made from the study of salinity and temperature observations.

The Rennell Current question is briefly considered.

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Replacement of Potassium by Rubidium in *Nitzschia closterium.*

By

F. A. Stanbury, M.Sc.

With 2 Figures in the Text.

VARIOUS attempts have been made to substitute certain elements for those acknowledged as essential for plant growth. Using plant material, sodium is the element usually chosen as a possible substitute for potassium, but results show that whilst sodium may be taken up in fairly considerable quantities this is only possible if small amounts of potassium be present as well. Total replacement appears to be impossible (**11**, **13**, **15**).

The failure to substitute sodium is not really surprising, for although there is considerable likeness, there are important differences between the two elements. A substance more nearly approaching potassium is the element rubidium. Rubidium can only with great difficulty be distinguished chemically from potassium. Apart from the differences of their absorption spectra—differences which are not altogether reliable when dealing with very small amounts of these elements or when in the presence of other substances (**10**)—the only means of clearly distinguishing between them appears to lie in the differences between the properties of such complex substances as their meta-stannates or the tetra-thio carbamides of their respective iodides (**10**, **5**, and **6**).

The possible substitution of rubidium was tried by Cameron (**8**) with remarkable success. He used plants of *Petroselinium sativum* grown from seeds in an artificial soil of alumina and charcoal. The alumina was stated to be free from potassium, as was the charcoal, which was obtained by the imperfect combustion of sugar, both substances having been tested spectroscopically. This artificial soil was contained in a vessel of block tin and " manured " with nutritive material containing no potassium. The seedlings were watered with a solution containing rubidium chloride. Plants producing seeds resulted from these experiments. Compared with normal control plants, the " culture " plants were not so robust, but the fact remains that a cultivated plant, in which potassium occurs in a very large proportion in the ordinary way, was grown to a state of maturity on soil free from this element. Other plants grown upon the same type of artificial medium and under identical conditions except that they were not watered with the rubidium chloride solution, very quickly died, so that it would seem that the rubidium really replaced the potassium, but as Cameron himself pointed out, it is very difficult to obtain exact results when using any of the higher plants. The seeds from which the plants were grown would contain a certain amount of potassium, and this amount, although small, might be sufficient to influence growth throughout life. In testing the ash of the matured " culture " plant Cameron reported that " minute traces " of potassium were present, and he considered that this had been derived from the seed from which the plant had been grown. To obtain really conclusive results the seeds of the " culture " plant should have been grown for a number of successive generations, for only thus would it seem possible to reduce the potassium present in the final plants to a minimum approaching elimination.

Using rubidium sulphate an attempt to replace potassium has now been made using the marine diatom *Nitzschia closterium* as the plant material. In this diatom, growth is relatively rapid, so that the products of several successive generations can be obtained in a comparatively short time. It could, therefore, be hoped to obtain by sub-culturing from normal parent stock, diatoms from which the element potassium was gradually eliminated.

The results of such experiments are presented in the following pages.

MATERIAL USED AND METHOD OF WORKING.

The stock material was that of a persistent culture of *Nitzschia closterium*, a marine diatom grown in sterilized natural sea-water to which nutritive material had been added in the form of " Miquel solution " (**17**). Artificial sea-water was made up according to the method described by Allen (**1**). All the elements of natural sea-water, excepting potassium, were present in their proper proportions. Nutrient material was added in the form of a modified " Miquel solution," the potassium salt again being omitted and substituted by one of sodium. The salts used were Kaulbaum salts, pure for analyses, or of the British Drug House—analytical quality : the water used was freshly distilled into Winchester quart bottles which had once contained strong acid, but which had been used for distilled water only for at least five years. All the ingredients were dissolved and kept in quartz vessels to prevent any possible contamination with potassium. The artificial medium gave no flame test for potassium with either the ordinary blue or with the didymium glass—a glass which transmits the blue freely whilst completely blocking the wave lengths emitted by sodium. The absence of potassium was also verified spectroscopically by a technique which was capable of detecting 2×10^{-5} mg. potassium per cubic millimetre, but failed to detect half of this amount.

This potassium-free (–K) artificial sea-water was sterilized, and 80 cubic centimetres of it were poured into a clear quartz flask and inoculated with a very small drop of Nitzschia culture containing a known number of diatoms per unit of volume. This sub-culture (A) was then covered with a quartz plate and kept sufficiently aerated, and placed in a window receiving light of a suitable intensity for diatom growth. The aeration of the sub-culture was effected by a sterilized pipette, which after sterilization had been rinsed in the sterilized potassium-free sea-water described. The counting of the diatoms was done with a hœmocytometer (**17**). In every case five counts were made and the figure recorded is the mean of five counts which were usually quite concordant.

A trace of potassium was naturally introduced with the inoculating drop. This, together with any traces of potassium present in the artificial medium, but not detectable by the spectroscopic method, was soon used up, as was indicated by the results of counting, since a point was reached where no further increase in numbers occurred. Table I. It was therefore assumed that the sub-culture A was now devoid of any available potassium. No further increase in numbers was recorded although the diatoms present appeared quite healthy, but a little smaller in size than the normal.

Using a new supply of potassium-free sea-water, a new sub-culture (B) was made from the potassium-depleted culture A. There was very little multiplication in the new sub-culture B as may be seen from Table II.

TABLE I.

TO SHOW THE GROWTH OF SUB-CULTURE A OF *NITZSCHIA CLOSTERIUM* TRANSFERRED FROM NORMAL SEA-WATER TO A POTASSIUM-FREE ARTIFICIAL MEDIUM.

Date.	No. of diatoms per unit of volume, viz. 0·1 mm³.
12.6.32	14
15.6.32	58
19.6.32	69
26.6.32	85
3.7.32	78
8.7.32	94
13.7.32	94
13.9.32	94

The spectroscopic test showed the medium to be free from potassium, although this test is really valueless at this stage, since growth did take place in the potassium-free medium in spite of its failing to show any trace of potassium by this test. At this point the sub-culture B showed

6×10^4 diatoms per cubic centimetre of solution, and the figure remained constant for a period of several weeks.

Sub-culture B was then shaken very thoroughly to ensure equal distribution of the diatoms throughout the medium, and divided into seven equal portions, each being poured into a small quartz crucible of ten cubic centimetres capacity. To six of the divided cultures known amounts of potassium or rubidium were then added, numbers 1, 2, and 3 receiving potassium as potassium sulphate and 4, 5 and 6 receiving rubidium as rubidium sulphate. Crucible 7 was left untouched (see Table III). The crucibles were then covered with quartz glass plates and set aside in the window, and aerated and counted in the usual way. The drops taken for counting were always rejected after use. The "1a," "2a" etc. crucibles refer to a second series done later.

TABLE II.

To show the Growth of Sub-culture B of *Nitzschia closterium* transferred from the Potassium-depleted Sub-culture A, to fresh Potassium-free Artificial Medium.

Date.	No. of diatoms per unit of volume (0·1 mm.^{3}).
16.9.32	New inoculation
30.9.32	3
6.10.32	5
14.10.32	6
21.10.32	6
28.10.32	6
28.11.32	6

RESULTS.

Two series of experiments were performed. The first series during the Winter and early Spring, November 28th–March 3rd, and the second during the Autumn, September 25th–November 24th.

Previous work with *Nitzschia closterium* has shown that the growth figures at any time of the year show peculiar rising and fallings, the cause of which cannot satisfactorily be explained (**17**). The cultures at present under consideration also show these irregularities (see Tables III and IV). With the exception of the untouched cultures 7 and 7a, all show increase in growth. In the first series of experiments, the increase is fairly steady for a period of fifty-one days, and towards the end of this time the figures tend to be proportional to the amount of potassium added in cultures 1, 2, and 3. The same tendency is shown in the potassium containing cultures of the second series. The extraordinary growth of culture 2, which received 10γK per c.c. of culture solution, can only be explained on the supposition that some impurity had inadvertently been admitted whilst extracting droplets for counting. Increase in temperature and in the length of the day as the year had proceeded could not alone account for such growth (Figs. 1 and 2.)

The continued fall in numbers in culture 3, after a very short growth period, is probably due to potassium starvation, and it would seem that the limiting value of potassium-requirement is being reached—viz. 4γK per c.c. of culture. The diatoms were small and in an unhealthy condition. A similar amount of rubidium in culture 6 gave slightly better growth throughout the course of the first series of experiments, and although the diatoms were small in size they appeared quite normal and healthy in form when seen under the microscope. Culture 4 shows the poorest growth, although it contains the largest proportion of rubidium, viz. 21γRb. per c.c. of culture solution. This amount appears to be injurious for continued growth. It therefore seems that, although rubidium may be harmful in certain proportions (culture 4), in smaller

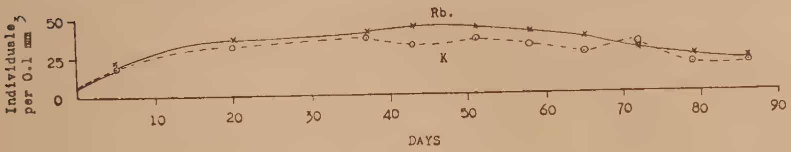

FIG. 1.

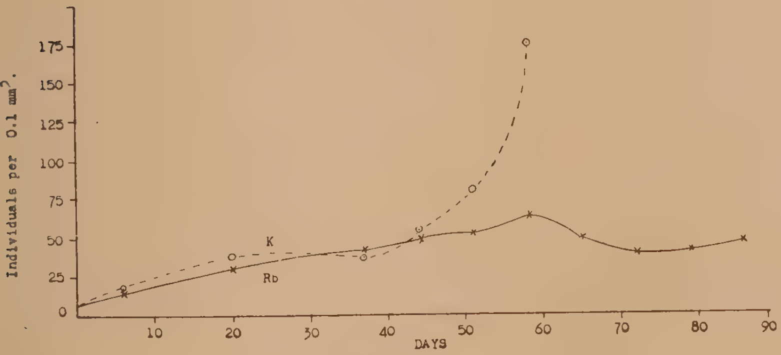

FIG. 2.

FIGS. 1 and 2.—Showing growth of *Nitzschia closterium* in artificial sea-water containing known amounts of potassium or rubidium respectively—viz. 4 micrograms of K. or Rb. in Fig. 1, and 10 micrograms of K. or Rb. in Fig. 2.*

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* In Fig. 2 the "potassium" curve shows abnormal growth after 51 days. This is probably due to some trace of impurity, possibly introduced during aeration of the cultures.

amounts (culture 6) it is quite as efficient as similar amounts of potassium, but even in that case increase is restricted to 7-11 times their original number.

TABLE III.

To show the Growth of the Sub-cultures of *Nitzschia closterium* when supplied with known Amounts of Potassium or Rubidium respectively shown as Micrograms per c.c. $(10^{-6}g=\gamma)$, over a Period of 86 Days. Nov. 28th–March 3rd (1932–1933)

		Numbers of diatom per 0·1 mm.³ of culture.						
Culture number		7	1	2	3	4	5	6
Date.	Days.	Untreated	21 γK	10 γK	4 γK	21 γRb.	10 γRb.	4 γRb.
28.11.32	Started	6	6	6	6	6	6	6
4.12	6	6	18	20	17	12	14	17
18.12	20	6	32	37	30	36	29	34
31.12	37	6	46	37	35	41	40	37
8.1.33	44	6	102	55	30	35	48	43
15.1	51	4	162	81	33	29*	52	42
22.1	58	6	‡	175	30†	26*	64	37†
29.1	65	6		350	25	20*	50	35
5.2	72	5		420	30*	20*	39	27
19.2	79	4		500	20*	20*	42	23
3.3	86	5			22*	18*	47†	21†

TABLE IV.

Amount of Potassium and Rubidium as above. Experiment conducted over a Period of 69 Days. Sept. 25th–Nov. 24th, 1933.

1933.	Days.	7a.	1a.	2a.	3a.	4a.	5a.	6a.
25.9.33	Started.	6	6	6	6	6	6	6
6.10	11	6	18	14	13	15	12	12
13.10	18	6	32	29	23	22	32	21
20.10	25	5	60	32	27	30	54	30
27.10	32	5	100	53	39†	44	66	43†
3.11	38	4	122	63	35	50	60	39
10.11	45	3	110	53	33	43	57	36
24.11	69	3	110	50	30	40†	58†	33†

In the second series the same general tendencies in growth are shown over corresponding periods of time, the greatest difference being the better growth of the diatoms supplied with most rubidium, viz. culture 4a supplied with 21γ rubidium per c.c. of culture medium (Table V).

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* Empty frustrules numerous. Culture obviously dying off.
† Frustrules healthy, but small in size.
‡ Culture found overturned.

TABLE V.

To show the result of correlating numbers giving increase in growth and the available potassium or rubidium per diatom in gram atoms.

THE POTASSIUM-CONTAINING CULTURES.

	First series.			*Second series.*		
Number of culture	1.	2.	3.	1a.	2a.	3a.
Length of time in days	28.11.32–15.1.33 51 days.			25.9.33–10.11.33 45 days.		
Amount of potassium supplied in γ	21	10	4	21	10	4
No. of diatoms at end of period in 10^4 units	161	81	33	110	53	33
Amount of potassium in 10^{-14} gram per diatom	1·29	1·23	1·21	1·9	1·9	1·21
10^{-16} gram atoms of potassium per diatom	3·3	3·15	3·1	4·8	4·8	3·1

TABLE VI.

THE RUBIDIUM-CONTAINING CULTURES.

	First series.			*Second series.*		
Number of culture	1.	2.	3.	1a.	2a.	3a.
Length of time in days	28.11.32–15.1.33 51 days.			25.9.33–10.11.33 45 days.		
Amount of potassium supplied in γ	21	10	4	21	10	4
No. of diatoms at end of period in 10^4 units	29	52	42	43	57	36
Amount of rubidium in 10^{-14} gram per diatom	7·2	1·92	0·91	4·9	1·75	0·11
10^{-16} gram atom of rubidium per diatom	8·5	2·25	1·07	5·76	2·06	1·3

Tables V and VI show the results of correlating the figures of increase in numbers, with the amounts of available potassium or rubidium present in the two series after periods of 51 days and 45 days in the first and second series respectively. During these times growth had been fairly regular and steady in the two sets of experiments.

From these figures it will be seen that the individual diatom requirement is approximately $1{\cdot}3 \times 10^{-14}$ gr. K. per unit. Using this figure it is therefore possible to estimate the amount of undetectable potassium present in the so-called potassium-free artificial medium. Reference to Table II shows that this artificial medium gives an increase of growth, reaching 6 diatoms per 0·1 mm.^{3} of culture medium. The potassium impurity must therefore approximate 0·78 micrograms per litre of solution.

It is also interesting to compare the potassium requirement of the diatom with the corresponding phosphorus need. Atkins has shown (**4**) that in fresh cultures, 1·12 mg. phosphorus as P_2O_5 will produce 1×10^9

diatoms. The phosphorus per diatom in gram atom obtained from this figure is $15{\cdot}8 \times 10^{-15}$ gram atoms as compared with $3{\cdot}3 \times 10^{-16}$ gram atoms potassium per diatom. The phosphorus-potassium ratio is therefore approximately 50.

CONCLUSIONS.

1. It is fully realised that the difficulty in detecting potassium and rubidium when present in small quantities and together with salts of sodium, is very great. The spectroscopic method used for the detection of these elements reached its limits of delicacy between 21 and 10γ potassium per c.c. in artificial sea-water.

It is calculated from the diatom growth recorded that the undetectable potassium was about 0·78 γ per litre.

2. That the growth recorded in the rubidium-containing cultures 4, 5 and 6 is not due to undetectable amounts of potassium present, as an impurity in the rubidium sulphate is fairly obvious when it is considered that the actual amounts of rubidium provided were 21, 10 and 4γ per c.c. of culture medium respectively. In view of the tested standard of purity of the chemicals used, it follows that any trace of potassium introduced, must of necessity be very small. Yet in the experiments 3 and 3a which received 4γ *potassium* per c.c. growth was no better than that of cultures 6 and 6a which received a similar amount of *rubidium*.

3. It may be concluded that when rubidium is supplied in small amounts (see cultures 6 and 6a) this element equals in efficiency similar amounts of potassium (see cultures 3 and 3a). In larger amounts, e.g. 21γ rubidium per c.c., rubidium would appear to be harmful. The diatoms in the rubidium-containing cultures seem to be limited to an increase of seven to eleven times their original number, so that even when the rubidium is not harmful the total replacement of potassium seems impossible.

4. It would seem that $3{\cdot}1 \times 10^{-16}$ gram atoms of potassium per diatom is approaching the limiting value of this element for the continued growth of *Nitzschia closterium*. For rubidium the corresponding figure is about $1{\cdot}1$–$1{\cdot}3 \times 10^{-16}$ gram atoms of rubidium per diatom.

5. Comparing the phosphorus requirement of *Nitzschia closterium* with that of its potassium need, the ratio of phosphorus-potassium is approximately 50.

I am greatly indebted to Dr. E. J. Allen for laboratory facilities and to Dr. W. R. G. Atkins for suggesting and directing the subject of the research and for his help and encouragement throughout the experiments.

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Abstracts of Memoirs.

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Pinnotherion vermiforme Giard and Bonnier, an Entoniscid infecting *Pinnotheres pisum.*

By D. Atkins.

Proc. Zool. Soc., Lond., Part 2, 1933, *pp.* 319–363.

Pinnotherion vermiforme infects *Pinnotheres pisum* from the Camel Estuary, Padstow, North Cornwall.

The males are not restricted in their occurrence to the body of the female, as apparently they are in other genera of Entoniscidæ, but occur isolated in the host, as do also the cryptoniscan larvæ. Of the total Pinnotheres examined 27·69% were infected. Infection with the male parasite alone was 26·85%, with the female (sometimes with males present in addition) 0·84%. The proportion of the sexes in *P. vermiforme* was 97·67% males and 2·33% females. The presence of the adult female causes partial to almost complete atrophy of the gonad of the host. At Padstow the female parasite has been found in the female host only; the male has on two occasions been found in the male host.

The relation of the parasite to its host and the possible manner of respiratory exchange is discussed.

The female and male *P. vermiforme* are described and figured, and, so far as material allowed, the epicarid and cryptoniscan larvæ.

D. A.

The Photo-electric Measurement of the Penetration of Light of Various Wave-lengths into the Sea and the Physiological Bearing of the Results.

By W. R. G. Atkins and H. H. Poole.

Phil. Trans. Roy. Soc. B., 1933, *Vol.* 222, *pp.* 129–164.

Using a potentiometer-telephone method with sodium, potassium and thin film caesium cells, and light filters, the coefficient of absorption was found to be: for the near ultra-violet, 0·390; blue, 0·140; green, 0·155; yellow (not including red), 0·164; orange-red, 0·435; red, 0·480 and deep red, 0·567. It follows that the sub-surface illumination is reduced to 0·001 per cent at 30, 82, 74, 70, 26, 24, 20 metres, respectively. The figures given may be taken as typical of the English Channel ten miles out. For the clearest water found, twenty miles from land, the coefficient was 0·077, for blue light. Correction factors are given for certain reflection losses between air-glass and air-water surfaces and for instrumental effects. The loss at the air-water surface appears to be small in calm water, but is appreciably increased by wind.

The heating of the water below the thermocline may be attributed to the absorption of light, from yellow to violet.

The ratio of the total vertical to the diffuse vertical light, in air, increases from 2·2, for near ultra-violet, to 5·5 for deep red, as determined under a clear blue sky with sun at 52° altitude.

Data, available from the work of Marshall and Orr, for the evolution of oxygen by diatoms, yield values for the absorption coefficient chiefly between 0·15 and 0·20, corresponding to that for light from blue to yellow.

The spring increase in diatoms was not found to decrease light penetration. At a maximum the mean thickness of diatoms traversed in a 10 m. water column is only 0·25 mm. and is probably nearer one-tenth of that on an average.

The absence of red light from the deeper water may be expected to have a bearing on the colour vision of certain fish.

Hulburt's coefficients have been used to show that even in the clearest ocean water the anti-rachitic portion of the spectrum is reduced to 1 per cent of its sub-surface value at 1·1 2·2 m., according to wave-length and to 0·001 per cent at from 2·9 to 5·5 m. This has an obvious bearing on the origin of vitamin D in fish-liver oils.

W. R. G. A.

Osmotic and Ionic Regulation in the Shore Crab, *Carcinus maenas*, with notes on the Blood Concentrations of *Gammarus locusta* and *Ligia oceanica*.

By J. B. Bateman.

Journ. Exp. Biol., Vol. X, 1933, *pp.* 355–371.

Chloride and vapour pressure data for the body fluids of Carcinus living in various strengths of sea-water were obtained, Duval's observation that " osmotic " regulation is abolished in concentrated sea-water being confirmed. Then the effect of " osmotic " and " ionic " forces on the normal regulation was studied by immersing crabs in sea-water containing respectively foreign non-electrolytes and electrolytes. The substances added showed interesting specific effects, glucose in particular causing a large increase in blood chloride, but in general they supported the belief that the regulating membrane (presumably the gill) is impermeable to water. This is in agreement with other experiments which are described. Miscellaneous experiments on the effects of cyanide, pH, and temperature are given, with a discussion of the mechanism of regulation and the thermodynamic work involved.

A direct study of the body fluids demonstrated the high degree of osmotic independence of Ligia for short periods of immersion and its breakdown after longer periods. Gammarus appears to regulate in much the same way as Carcinus.

J. B. B.

The CO_2 Dissociation Curves and the Buffering of Crab's Muscle and Nerve Preparations.

By S. L. Cowan.

Journ. Exp. Biol., Vol. X, 1933, *pp*. 401–411.

Crab's muscle and nerve preparations, which had been previously soaked in aerated sea-water for an hour, were brought into equilibrium with different CO_2 nitrogen mixtures of known composition in a modified Barcroft apparatus and then the combined CO_2 was measured after acidifying the tissue. From the CO_2 dissociation curves so obtained, by means of the Henderson-Hasselbalch equation, the pH of the preparations under known CO_2 pressures was calculated.

For muscle and for nerve the relation between CO_2 pressure and cH was almost linear over the greater part of the range.

It is probable that the CO_2 binding capacities and the pH of the tissues are altered by the preliminary soaking in sea-water, and that the figures given would not hold good (for muscle and nerve) in the intact animal.

S. L. C.

The Relation between Somatic and Germ Cells in the asexually produced polyps of the Polyzoan *Alcyonidium gelatinosum.*

By G. H. Faulkner.

Annals and Magazine of Natural History, Ser. 10, *Vol. XI*, 1933, *p*. 255.

In the development of the asexually produced polyp of *Alcyonidium gelatinosum*, certain cells are very early set aside, and remain undifferentiated. They proliferate actively, and contribute to the growth of the alimentary canal ; during the period of growth they form a morula-shaped mass projecting into the body cavity, attached to the cæcum of the alimentary canal adjacent to the attachment of the funiculus. In the sexual season cells persisting from this group give rise to the female sex-cells. (The origin of the male germ-cells was not traced.) These cells are inter-epithelial in position, lying between the basement membrane of the endoderm and the peritoneum. They are considered to be homologous with the neoblasts of Annelids.

G. H. F.

Recherches Sur les Hemérythrines.

By Marcel Florkin.

Arch. Int. Physiol., 1933, *Vol.* 36, *pp.* 247–328.

The haemerythrins, respiratory proteins found in the red cells in the cœlomic fluid of the Sipunculids, are typical globulins, crystallizing in the rhombohedric system. The spectrum of the haemerythrin of *Sipunculus nudus* is quite different from the spectra of all haem derivatives, and in ertain aspects more similar to the Haemocyanin (hemsbyanius) spectrum. The ratio $\frac{\text{Iron}}{\text{Oxygen}}$ is different from this ratio for the oxygenation of Haemoglobin. In conditions where Haemoglobin is transformed into Carboxy-haemoglobin, there is no combination of CO to Haemerythrin. The respiratory function of the cœlomic fluid of *Sipunculus* is analysed, and the Bohr effect shown to be absent. The different peculiarities of this cœlomic fluid show many correlations with the characters and habits of the animal considered.

M. F.

Blood Circulation of Animals possessing Chlorocruorin.

By H. Munro Fox.

Proc. Roy. Soc., Ser. B Vol. CXII, 1933, *pp.* 479–495 .

Most blood-vessels of sabellids and serpulids are rhythmically contractile, including all the blind-ending capillary vessels in crown, body wall, and coelom. In the continuous vessels the blood is circulated by peristalsis, in the capillaries there is an ebb and flow of the blood. The rhythmic contractions of the vessels are independent of the central nervous system. The simultaneity of contractions in the vessels of the separate filaments of the crown is controlled by a ganglion at the base of each half of the crown. After sabellid worms have retired into their tubes for over half an hour, the contractions of their blood-vessels cease. The contractions recommence as soon as even the tip of the crown projects beyond the end of the tube. In spite of the cessation of blood circulation, Spirographis can remain uninjured for eight hours in its tube when the latter is artificially closed. After eight hours the animal makes a new anterior lateral opening in the closed tube and re-expands its crown. When sabellids or serpulids, removed from their tubes, are put into sea-water the pH of which has been brought below 6·0 by the addition of carbon dioxide, the contractions of their blood-vessels stop. Neither water acidified with hydrochloric acid to the same pH as the water containing carbon dioxide, nor water lacking dissolved oxygen, produces this effect. The inhibition of blood-vessel contractions due to carbon dioxide is reversible when the animals are replaced in pure sea water. Carbon dioxide does not inhibit the blood-vessel contractions through a nervous reflex, it causes an internal accumulation of carbon dioxide which acts directly on the blood-vessel walls. It is probable that the cessation of blood-vessel contractions when sabellids have retired into their tubes is due to the accumulation of carbon dioxide in the water between the filaments of the crown. The threshold pH for the inhibition of blood-vessel contractions of Dasychone was determined in (*a*) sea-water containing dissolved carbon dioxide, (*b*) sea-water of abnormally high alkali reserve containing carbon dioxide, and (*c*) sea-water acidified with hydrochloric acid. From these data it was concluded that both carbon dioxide and hydrogen ions are concerned in the inhibition, but that the former is more important than the latter. Carbon dioxide also causes the reversible inhibition of contractions in the following cases: (*a*) the dorsal blood-vessel of Nereis; (*b*) the hearts of Daphnia, Artemia, Chlœon nymphs, Phallusia, chick embryos; (*c*) the contractile vesicles of Limax embryos.

H. M. F.

Einige Untersuchungen über die Eiweissverdauung bei Gastropoden.

By Sven Hörstadius.

Biologisches Zentralblatt, Vol. 53, 1933, *pp.* 645–650.

The investigation was made in Utrecht, Naples, and Plymouth, the last place thanks to a Ray Lankester Investigatorship. Several statements of phagocytosis in Gastropods have proved to be wrong. Previous investigators found ingested carmine particles in mid-gut gland cells (Helix, Planorbis). A close examination shows that, instead, granules in the cells have been stained red by carmine, that has gone into solution and thus passed into the cell by means of diffusion. Proteolytic enzymes are active in the gut, as fibrin is dissolved. Colloidal gold particles of a certain size, embedded in small pieces of fibrin, were never ingested by the cells.

Also the previous result, that chloroplasts are ingested by Aplysia cells, has proved to be based on a mistake. No phagocytosis takes place, but chlorophyll diffuses into the cells and stains granules green and brown.

On the other hand, phagocytosis was stated to occur within Pleurobranchea, by aid of the gold particle method, and within Hermæa. The latter was fed partly on Codium, partly on Bryopsis, two algæ with chloroplasts of very different size. Both kinds of chloroplasts were found in the liver cells.

S. H.

On *Ceratotrema Furcolabiata* n.g. et n.sp. and *Hemipera sharpei* n.sp. Two New Digenetic Trematodes of British Marine Fishes.

By E. Idris Jones.

Parasitology, Vol. XXV, 1933, *pp.* 248–254.

(*a*) *Ceratotrema furcolabiata* n.g. et n.sp. was found in the cœlom of *Onos mustela* at Plymouth. This is the third trematode recorded from the cœlom of fishes.

Generic Diagnosis. Length 7·3–7·8 mm. Greatest width 1·7 mm. Abdomen completely invaginated into body. Anterior sucker approximately two-thirds size of ventral sucker ; average measurements 0·57 and 0·77 mm. respectively. Anterior sucker with three cushion-like projection into lumen, one anterior and two postero-lateral. Lip dorsally situated, very muscular, and strongly bifid, not overhanging the mouth. Ventral groove present. Testes two, oval, situated opposite each other immediately posterior to ventral sucker. Ovary spherical, posterior to testes. Receptaculum seminis present. Vitellaria arranged in two groups posterior to ovary ; limbs of vitellaria short and thick and split up to base. Metraterm long, reaching almost to ventral sucker. Eggs green, numerous, $23\mu \times 11\mu$.

Host ; *Onos mustela*, in cœlom. Types in the British Museum (Nat. Hist.). Its systematic position is indicated.

(*b*) *Hemipera sharpei* n.sp. Found under the operculum of *Cepola rubescens* at Plymouth.

Specific Diagnosis. Host ; *Cepola rubescens.* Situation ; under gill-cover. Large and robust. Bluntly rounded. Length, 4·77–4·85 mm. Anterior sucker, 0·372 mm. Ventral sucker, 0·744 mm. Laurer's canal present and prominent receptaculum seminis. Eggs not curved and with long filaments not intertwining. Egg measures $100\mu \times 38\mu$.

E. I. J.

Fertilisation and Egg Formation in a Digenetic Trematode, *Podocotyle atomon.*

By E. Idris Jones.

Parasitology, Vol. XXIV, 1933, *pp.* 545–547.

An account is given of the fertilisation of the ova and of subsequent egg formation in *Podocotyle atomon.* The times taken for the various processes are given.

E. I. J.

Studies on the Monogenea (Trematoda) of Plymouth. *Microbothrium caniculæ* (Johnstone, 1911).

By E. Idris Jones.

Parasitology, Vol. XXV, 1933, *pp*. 329–331.

Microbothrium caniculæ was found at Plymouth for the first time on *Scyllium canicula.* It had previously been described by Johnstone as *Paracotyle caniculæ* n.sp. in 1911. A detailed description of the morphology of the species is given and its position in the genus *Microbothrium* Olsson 1869 indicated. E. I. J.

The Hirudinea of Plymouth. Part I.

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXV, 1933, *pp*. 255–262.

This account deals with the Ichthyobdellidæ. A list is given of those hitherto found at Plymouth, and a description: of some presumably young forms found on skate: of two new species, *Branchellion borealis*, having but 31 pairs of gills, one specimen, taken by Mr. G. A. Steven on a skate; and *Janusion scorpii*, perhaps the *Platybdella scorpii* of Malm, occasionally found by the author on *Cottus scorpius.* W. H. L.-S.

Studies on the Relation between Organism and Environment.

By J. H. Orton.

Transactions of the Liverpool Biological Society, Vol. XLVI, 1932, *pp*. 1–16.

In this short paper a summary is given of the author's experiments and observations on marine animals which demonstrate differences in the manifestation of the fundamental processes of feeding, growing, breeding, sex, and survival in different environments. It is therefore adduced that variation in the environment—and still more permanent non-lethal changes—may be expected to bring about definite changes in the organism. From the general fitness of the organism to the environment it would appear that such adaptive changes have become fixed in some manner which still remains to be demonstrated.

The author gives some hitherto unpublished observations on the characters of shells of *Patella vulgata* L.* The notably wide range of variation at all sizes in the relation between the mean of the length (L) and breadth (B) of the shell—and height (H)—is shown.

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* The adults (i.e. with shells above about 3 cm.) were normal common limpets; many colour varieties occurred among the young individuals and traces of the coloured rays could be seen in the smaller thin-shelled low-water adults. There does not appear to be any valid reason for recognising the low-water form from this locality as the separate species, *P. intermedia* Jeffries. Typical forms of the variety (or species) *P. athletica* Bean do not occur in the locality in the habitats sampled. (See *Journ. Mar. Biol. Assoc.*, N.S., Vol. XV, p. 860.)

A close comparison of samples of limpet shells from respectively high- and low-water situations on Looe Island is made, and constant differences are demonstrated in the following relations: length and height; length and mean axis (mean axis $= \frac{L+B+H}{3}$); length and weight; approximate internal area of shell and weight at given corresponding lengths; weight and apical thickness of the shell for given lengths. The latter values are higher in all cases for high-water limpets.

The shape of a sample of shells of a given range in size is definable by the numerical value of the mean $\frac{L+B}{2H}$, which is given for a number of samples from high- and low-water situations; the low-water samples give values constantly higher than those from high water. The high-water samples were taken from various selected situations on the south coast of England; it was found that the greater the exposure of the shells to dessication the lower was this numerical value for shell-shape. In an examination of limpet habitats extending over a large portion of the coast of Devon and Cornwall, this effect of dessication was confirmed except for a small population of limpets on an island adjacent to the Gas Works, Teignmouth Estuary, where relatively tall shells are found at about high-water neaps.

The explanation is offered that the shape of the shell in any habitat is due ultimately to habit; in situations exposed to dessication the animal must cling tightly to the substratum to maintain a moist condition of the gills, in damp situations the animal does not need to remain apposed to the substratum; these habits are known. Since increase in shell area occurs at the edge of the shell, and limpets may be assumed to grow shell while apposed to the substratum, a smaller perimeter increment of growth will be made by an apposed limpet than by one relaxed or not apposed. Hence limpets more constantly apposed to the substratum grow a higher shell than those relaxed in damp situations.

Different laws of growth are indicated for young and older individuals; first approximations are given. The studies are being continued, and other results will be communicated later.

J. H. O.

Experiments on the Suitability of some Rectifier Photo Cells for the Measurement of Daylight.

By H. H. Poole and W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1933, *Vol.* 20, *pp.* 537–546.

In using rectifier cells it is necessary to know the form of the current illumination curve. The latter depends on the resistance of the external circuit, so a low resistance galvanometer should be used. A shunt was designed to reduce the galvanometer sensitivity without affecting its resistance. Temperature effects are important in some cells. The wavelength sensitivity curves of several cells were studied, that of the Bergmann selenium cell is by far the closest in form to that of the human eye. This selenium cell is also relatively the most stable.

W. R. G. A.

Reversal of the Current from a Cuprous Oxide Photo Cell in Red Light.

By H. H. Poole and W. R. G. Atkins.

Nature, 1933, *Vol.* 131, *pp.* 133 *and* 547.

The effect, observed by Auger and Lapicque, was found to exhibit a maximum at 6280 A. In the marginal region of the cell it amounted to 10·6 per cent of the maximum sensitivity of the cell for the direct current, which occurred near 5000 A. The central region gave no reversal. The explanation offered is that the normal effect is located at the front surface of the copper-oxide film, whereas the reverse effect is due to red light penetrating the film to the copper plate behind, but only where the film is thin, as at the margin. The values relate to an equal energy spectrum. At one spot in the marginal region the reverse effect was 28·5 per cent of the maximum direct current from the same region.

W. R. G. A.

BOOK NOTICE

Arachnoidiscus. An account of the genus, comprising its history, distribution, development and growth of the frustule, structure and its examination and purpose in life, and a key to and description of all known species, illustrated.

By N. E. Brown, D.Sc., A.L.S. London, W. Watson & Sons, Ltd., 1933. Price 6s. net.

Dr. Brown, who is a well-known expert with the microscope, has given us a valuable addition to our knowledge of diatoms, and his book on this one beautiful and important marine genus, both recent and fossil and of world-wide distribution, is most interesting, being a detailed study of all the species, 26 altogether. Microscopists are familiar with *Arachnoidiscus* because of its exceptionally intricate and elaborate structure with rays and meshes not unlike a spider's web, hence the name. Apparently up to the present time the nomenclature has been much confused and the species very inadequately described. This is now put right and most of the species found to have a definite distribution confined to particular areas, one species only (*A. anatus*) being widely distributed.

Perhaps the most interesting part of the work is the description of the male and female frustules, for we know so little of this side of the life of any diatom.

The photographic figures illustrating the volume are very clear and good.

M. V. L.

Marine Biological Association of the United Kingdom.

Report of the Council for 1933.

The Council and Officers.

The Council has held four meetings in London during the year at which the average attendance has been seventeen. These meetings took place in the Rooms of the Royal Society at Burlington House and the thanks of the Association are due to the President and Council of the Royal Society for the accommodation provided. A Committee of the Council, consisting of eight members, including the Chairman of Council, Prof. E. W. MacBride, F.R.S., visited and inspected the Laboratory at Plymouth on April 8th.

The Council has to record with deep regret the loss by death, since the last Annual General Meeting, of Sir William Hardy, a Vice-President of the Association, who as Chairman of the Advisory Committee of the Development Commissioners, by his interest in the work at Plymouth and his constant advice and help, had done much to make possible the progress of the Laboratory during the last ten years; of Professor G. C. Bourne, for many years a Governor of the Association representing the University of Oxford and a former Director of the Plymouth Laboratory; of Mr. Nigel O. Walker, Honorary Treasurer of the Association since 1931; and of Mr. George Evans, who had served the Association for sixteen years, from 1915 to 1931, as Honorary Treasurer.

The Plymouth Laboratory.

The Laboratory buildings and fittings have been kept in a good state of repair and the paintwork in good condition. A ladies' cloak-room has been constructed in part of the former library in the main building, and alterations have been made to the store in order to preserve the interior woodwork from the effects of damp. In connexion with extensions made by the Plymouth Corporation to the Tinside Bathing Pool below the Laboratory, the pipe lines for water from, and for compressed air to, the ejector have been in part relaid and renewed, at the expense of the Plymouth Corporation.

The Aquarium.

The Aquarium has been maintained in an attractive condition and the number of visitors has increased. A number of parties of school children, in charge of their teachers, have studied the animals in the tanks. Notable exhibits have been some Electric Rays, chiefly *Torpedo nobiliana*, but one specimen of *T. marmorata*. These Electric Rays have lived well. *Octopus vulgaris* became common during the latter part of the summer and several fine specimens have been shown in place of the usual *Eledone cirrosa* which has been scarce. Unusual captures for the district were two Sea Horses (*Hippocampus guttulatus*), one of which survived for some time, being fed daily on planktonic copepods.

The Ship and Motor-Boat.

On the 7th June last the steam-drifter " Salpa " was placed on the slips in Hawke's shipyard, Plymouth, in order to undergo Lloyd's regulation half-time survey and to have the tail shaft drawn for inspection. The old shaft—the original one—proved to be much worn and a new tail shaft had to be fitted. In the course of the hull survey some of the woodwork was found to have deteriorated somewhat rapidly since the full-time survey in the winter of 1929-30, and a considerable amount of renewal of wood was ordered by Lloyd's surveyor as a condition for the continuance of the ship's character in the Society's Register Book. The necessary repairs were carried out, and at the same time a new lavatory was fitted, the old one having been completely worn-out. The ship is now in good order and remains in Class A 1 for the remainder of the seven-year period which commenced in March 1929.

The motor-boat " Gammarus " has worked continuously throughout the year with the exception of one month in August when the 6-H.P. " Kelvin-Ricardo " engine was removed and despatched to the makers for examination and overhaul. For some time previously this engine had not worked satisfactorily and neither the local agent nor the company's engineer could ascertain the cause of the trouble. The Bergius Company offered, therefore, to carry out an exhaustive overhaul and fit new cylinders free of charge—as the old ones had shown abnormal wear. This engine is now working satisfactorily. The 3½-H.P. engine, which had given continuous service in the " Gammarus " for eleven years, has been taken out and its companion engine, which was removed and stored when the 6-H.P. engine was installed, has been put back in its place.

The Staff.

Dr. L. E. Bayliss of the Physiological Laboratory, University College, London, was appointed to succeed Dr. C. M. Yonge as Physiologist at the Plymouth Laboratory, and commenced his duties in April.

Mr. O. I. Green, after completing one year as Student-Probationer, left at the end of September to take up the study of medicine in London.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

Dr. H. K. Adams, London (Blood of animals, especially Crustaceans).
Miss D. Atkins, London (Lamellibranch gills).
E. H. F. Baldwin, Cambridge (Bases of Cephalopod muscle).
Miss E. G. Barber, Portsmouth (Invertebrate mud fauna).
Miss F. L. Beanland, Portsmouth (Invertebrate mud fauna).
Miss A. M. Bidder, Cambridge (Digestive system of Cephalopods).
Miss M. V. Bishop, London (Yolk absorption in Purpura).
Dr. A. Brinkmann, Bergen (Laboratory Equipment and Methods).
Dr. S. C. Brooks, California (Library).
Dr. D. L. Bryce, London (Marine Rotifers).
E. Bushra, Cairo (Oceanographical Chemistry).
H. M. E. Cardwell, London (General Zoology).
Dr. and Mrs. J. ten Cate, Amsterdam (Reflexes of spinal cord of Dog-fishes).
F. A. Chrenko, London (Turbellaria).
H. O. J. Collier, Cambridge (Blood system of *Phallusia mammillata*).
S. L. Cowan, London (Chemical exchanges in Maia nerve. Action of drugs on Maia nerve).
G. I. Crawford, Cambridge (Ascidians).
Dr. A. Dannevig, Arendal, Norway (General Zoology).
J. H. Day, Liverpool and South Africa (Development of Polychæta).
R. Dennell, Manchester (Feeding mechanism of Crustacea).
Dr. M. G. Eggleton, Edinburgh (Chemistry of foot muscle of Mytilus).
Dr. P. Eggleton, Edinburgh (Isolation of Arginine phosphate).
Lt.-Commander W. I. Farquharson, Murray Expedition (Oceanography).
H. C. Gilson, Cambridge (Oceanographical Chemistry).
Dr. R. Gurney, Oxford (Plankton. Fish Parasites).
Prof. C. R. Harington, London (Inspecting raft of Civil Engineers' Institute).
Miss E. Harling, Looe (General Zoology).
T. J. Hart, "Discovery" Expedition (Plankton and Oceanography).
Prof. L. A. Harvey, Exeter (Asterina).
Dr. A. B. Hastings, London (Tunicates and Polyzoa).
Miss G. Hess, Zürich (General Zoology).
Prof. L. T. Hogben, London (Chromatophores of Mysis).
Dr. H. R. Ing, London (Action of drugs on Maia nerve).
Miss P. M. Jenkin, Cambridge, Ray Lankester Investigator (Correlation of photosynthesis of diatom cultures in the sea with photoelectric measurements of light penetration).
J. A. Kitching, London (Physiology of contractile vacuoles).
W. H. Leigh-Sharpe, London (Parasitic Copepods).
A. G. Lowndes, Marlborough (Polygraphic investigations of swimming movements of Copepods).
Dr. and Mrs. R. J. Lythgoe, London (Visual purple of fishes).
J. D. Macdonald, Aberdeen (Larvæ of Pagurids).
G. I. Mann, Plymouth (Mollusca).
A. F. Mohamed, Cairo (Oceanographical Chemistry).
Miss L. A. Morgan, Exeter (Turbellarian embryology).
Miss O. S. Mundy, Bristol (Gastric shield of Lamellibranchs).
Miss G. L. Naylor, London (Marsh Fucoids of St. John's Lake).
Dr. O. C. Neilson, Copenhagen (Preservation of nets, etc.).

G. E. Newell, London (Morphology of Melinna).
J. V. V. Nicholls, Montreal (Studies on the nerve in smooth-muscle preparations from the Ray).
Dr. E. A. T. Nicol, Edinburgh (Brackish-water fauna).
Dr. W. Nolte, Kiel (Polychæte larvæ).
Miss E. M. Oliver, London (Digestion in Gunda).
Dr. H. H. Poole, Dublin (Photo-electric measurements).
Dr. M. Ramult, Cracow (Development in Rhizocephala. Planktonic Crustaceans).
Dr. H. Rosenberg, Berlin and London (Fatigue of nerves of crabs).
Miss M. L. Rothschild, London (Parasites of Turritella).
D. Scott, London and New York (Fatigue of nerves of crabs).
H. R. Seiwell, Woods Hole, Mass. (General Zoology).
Dr. C. J. Shen, London (Life history of crabs).
F. G. W. Smith, London (Patella development).
H. G. Smith, Bristol (Chemistry of sea-water).
J. E. Smith, Manchester (Development of Cephalothrix).
S. Smith, Cambridge (Total nitrogen excretion of Carcinus).
Miss F. A. Stanbury, Plymouth (Growth of Diatoms).
F. C. Stott, Southampton (Phosphate and salinity methods).
Dr. S. Takatsuki, Tokyo (Physiology of the Oyster).
Dr. E. F. Thompson, Cambridge (Inorganic constituents of invertebrate blood. Oceanographical Chemistry).
Dr. R. Tourky, Cairo (Oceanographical Chemistry).
R. C. Vernon, Plymouth (Mollusca).
Mrs. D. P. Wilson, Plymouth (Marine algæ).
Dr. F. R. Winton, Cambridge (Excitability of foot muscle of Mytilus).
Prof. C. M. Yonge, Bristol (Crustacean chitin).
J. Z. Young, Oxford (Innervation of the viscera of fishes).

The usual Easter Vacation Course in Marine Zoology was conducted by Mr. D. P. Wilson and Mr. G. A. Steven, and was attended by forty-six students from Oxford, Cambridge, London, Edinburgh, Aberdeen, Liverpool, Sheffield, Newcastle, Birmingham, Reading, Hull, Huddersfield, Bognor Regis, and Bowden, Cheshire.

During the Summer Vacation, Professor J. H. Orton, of Liverpool University, with Miss R. Rawlinson and Mr. C. L. Smith as Demonstrators, conducted a Course in Marine Biology, which was attended by eighteen students from Cambridge, Edinburgh, Birmingham, Bristol, Bradfield, Plymouth, and Zürich, Switzerland.

Also during the Easter Vacation, Mr. J. M. Branfoot brought four students from Oundle School; Mr. B. A. Barr, two from Harrow; Mr. A. M. M. Gardiner, three from Radley College; Mr. A. H. Lewis, one from Wellington College; Mr. L. V. Turner, two from Rydal School; Mr. A. Gillespie, two from Westminster School; Mr. H. C. W. Wilson, ten from Monkton Combe; Mr. I. I. Hamilton, two from Dauntsey School, and Mr. C. B. Owen, three from Malvern College.

At Whitsuntide Mr. W. H. Leigh-Sharpe conducted a class of six students from the Chelsea Polytechnic.

The Scientific Work of the Plymouth Laboratory Staff.

The descriptions of the different investigations have again been arranged so as to indicate their bearing on the general plan of work that is being undertaken by the staff. The investigations on the physical and chemical characters of the environment are first described, then those on the vegetable and animal plankton, which form the basis of the food supply of the sea. Researches on the ecology, physiology, and genetics of the invertebrates of the sea-floor which feed on the plankton and on each other are then described. These invertebrate animals constitute the food of the bottom-living fishes and lead naturally to an account of studies on the fishes themselves and the commercial fisheries.

Physics and Chemistry of the Environment.

The productivity of the sea depends ultimately upon the amount of light available for photosynthesis. The seasonal changes in plankton are therefore dependent upon seasonal variations in light intensity and upon the clearness of the water. Certain of the zooplankton are also influenced in their movements by the illumination. For these reasons Dr. W. R. G. Atkins, in collaboration with Drs. H. H. and J. H. J. Poole of Dublin, has devoted much time in recent years to photometry. A new variety of photo-electric cell of the emission type has been studied and all types of cell available have been standardized in terms of mean noon sunlight, and also of electric arc and bulb lamp light. An improved technique has been adopted, using a potentiometer and electrometer valve null method of measuring the current.

The recording of daylight, started in 1929, has been continued, and a selection of the daily records, together with the apparatus used for submarine photometry as devised by the two Pooles, was lent to the Science Museum, London, for the Exhibition of Photo-Electric Apparatus. A study of the brightness of different parts of the sky has also been carried out.

The principal varieties of the rectifier type of photo-electric cell were also examined and a Bergman selenium cell was fitted into the submarine photometer instead of a cuprous oxide cell. There is a gain from this in stability, sensitivity and colour range. Moreover, as compared with the emission type, the limitations imposed by damp weather are removed and the closing shutter is rendered superfluous. The relation between current and illumination is, however, not rectilinear, so each rectifier cell requires to be calibrated for use in bright light. For work at sea the potentiometer amplifier null method can be used, but with a relatively low resistance.

Some measurements of submarine illumination were made in connexion with Miss P. M. Jenkin's work on diatom photosynthesis at various depths.

Hydrographic data in the mouth of the English Channel have been collected since 1921, and are now published in the Bulletin Hydrographique of the International Council. They are also worked up by Mr. H. W. Harvey. Charts of the surface salinity distribution at the mouth of the Channel are drawn for each month, utilising all available observations, and are reported upon in the Journal of this Association. The years 1931 and 1932 were remarkable for the presence of unusually high salinity water off the mouth of the Channel, patches of which moved up-channel at intervals. Salinities as high as 35·6 and 35·7 were met with on occasions, suggesting water of Mediterranean origin. The temperatures met with, on the other hand, were not extraordinary although the autumn of 1931 was marked by unusually warm water of rather low salinity.

Dr. L. H. N. Cooper has been seeking expeditious methods for determining small amounts of certain metals in sea-water. For iron, 2 : 2′-dipyridyl and Morgan and Burstall's newly discovered 2 : 2′ : 2″-tripyridyl have been found to be excellent reagents. With tripyridyl, samples containing 0, 1 and 2 mg. of iron per cubic metre can just be distinguished from one another. Ferric and organically bound iron have first to be converted to the ferrous state. A start has been made on a study of the seasonal changes in iron and also in copper in the Channel.

Delicate methods for ammonia have also been further investigated. Phenol in presence of hypochlorite gives a blue colour with ammonia, which will detect one part of nitrogen in twenty million parts of water. The reagent appears superior to the Nessler but is not quite sufficiently sensitive for work on sea-water.

The routine observations on the seasonal changes in phosphate have been continued.

Methods have been devised for the analysis of organic phosphate in sea-water and of phosphorus in plankton. In the top forty metres at Station L4 in October, when plankton was fairly abundant, the phosphate present in plankton organisms amounted to only 0·24 mg. P_2O_5 per cubic metre of water, which seemed surprising.

A tentative method for determining oxidisable organic matter in sea-water has been worked out, using solutions of dichloramine–T in acetic acid, which are reasonably stable, as an easily controllable source of chlorine, the absorption of which by the organic matter can be measured.

Measurements have again been made of the variation of excess base between the surface and bottom in the English Channel. These confirm last year's results that a very small difference exists due to a variation in calcium.

Five English and Egyptian members of the John Murray Expedition to the Indian Ocean visited the Laboratory during the Summer to familiarise themselves with chemical methods of analysis of sea-water and a good deal of time was spent by Dr. Cooper in helping them and in preparing reagents for the expedition.

Plankton.

In continuation of investigations on factors influencing the productivity of the sea—the supply of nutrient salts, hydrographic conditions and growth of diatoms—Mr. H. W. Harvey has devised a rapid method of assessing the plant pigments, and hence the phytoplankton, per cubic metre of water. A water-meter has been constructed which measures the quantity of water which has passed through a silk net while being lowered and hauled vertically through the sea. The catch is filtered on a silk disc and the yellow-green plant pigments dissolved in acetone. The resulting green solution is compared with colour standards. After various trials at Plymouth the meter was calibrated at the National Physical Laboratory for rates of water flowing through it varying between 47 and 550 litres per minute. The quantity of water which passed through and registered a unit division on the dial varied between 11·4 and 12·2 litres, sufficient constancy for practical purposes. Similar meters have now been made by London firms for the *Sir John Murray* and *Discovery II* expeditions. A closing mechanism actuated by messengers, has been evolved, which allows the gear to be fished between any two desired depths or to be hauled horizontally from a heavily weighted line.

Quantitative vertical hauls with a 200 mesh silk net have been made by Mr. Harvey at frequent intervals from the ship and motor-boat mostly between Cawsand and the Eddystone. The diatoms in an aliquot portion of the catch were examined or counted, the remainder being used to estimate the content of plant pigment.

From winter values of 15 to 190 (arbitrary) units of plant pigment per cubic metre of water, a spring maximum of some 6900 units per m^3 was observed on March 28th. During this period the growth in the more turbid in-shore waters was less than further out to sea. Between March 28th and April 4th, there was a sudden fall to winter values in the clearer water out to sea and an equally sudden increase in the quantity of zooplankton, the fæcal pellets of which, consisting largely of diatoms, were present in great numbers. This condition of little plant life and much zooplankton persisted for about a month, although there was no scarcity of light or nutrient salts. During May a growth mainly of *Rhizosolenia alata* took place, some 4800 units of pigment per m^3 being observed on May 22nd. Meanwhile the quantity of zooplankton in the catches had diminished. This crop fell away to be replaced by a crop mainly consisting of *R. stolterfothii* in June. During July, August and early September plant life was very sparse and zooplankton rich. Then, coincident with a fall in the quantity of zooplankton, an autumn crop appeared consisting mostly of *Rhizosolenia styliformis* and *Biddulphia sinensis*. From this preliminary quantitative survey it appears that, except during the winter, the quantity of phytoplankton present at any one time is largely dependent upon the quantity of zooplankton feeding upon it, and not entirely dependent upon the available nutrient salts and amount of light. Observations made by this quantitative method and a consideration of the phosphorus contents of water and phytoplankton from Dr. Cooper's analyses, suggest that from April to October the sea was a closely grazed pasture, except for short intervals in May and June.

Mr. F. S. Russell has completed the working out of his material to study the biology of Sagitta, the general results of which were outlined in the last report. These results have been published in the Journal, Vol. XVIII, No. 2. He has also completed the working up of a series of collections showing the general seasonal distribution of ring-trawl caught plankton, the information from which was printed in the last number of the Journal and is to form a basis for the study of changes in abundance of different animals from year to year. In continuation of this research Mr. Russell has examined weekly catches of plankton from the ring trawl and recorded the occurrence of various animals of interest and more especially the medusa population, and the occurrence of Sagitta. It is noteworthy that *Sagitta setosa* is still predominating in the catches over *S. elegans*, and indeed in the autumn of this year (1933) it has entirely displaced the last-named species, no *S. elegans* having been seen for several weeks.

The working up of the collections made in the summer of 1931 to study the effect of light intensity on the vertical distribution of plankton animals has now been completed. In this study collections were made from several depths simultaneously, while, either just before or after, light intensity measurements were made at different depths by Dr. Atkins. Seven series of observations were made on five days in July and August. The behaviour of *Calanus finmarchicus* adult males and females has been studied in detail. It was found that the females in July were living in the upper water layers in light intensities of 20,000-metre candles and over, but that those in August were avoiding these high intensities. This change in behaviour was coincident with a change of size of the copepods and indicated that actually there had been a change in the population being sampled and that these two populations, which differed in the size of their individuals, differed also in their behaviour towards light intensity. Measurements showed that while in July the average length of the female Calanus varied between 3·141 and 3·186 mm., in August these lengths were only 3·000 and 3·068 mm. Similar differences were shown by the adult males, which in July avoided intensities of 40,000 m.c. and over, while in August their upper limit was about 10,000 m.c. The males were consistently slightly deeper in the water than the females but appeared to show a more even distribution between their upper and lower limits.

Dr. M. V. Lebour has continued her studies of planktonic gastropods which have proved increasingly interesting. A paper on the eggs and larvæ of the Plymouth Turridæ is now ready for publication. These are very important members of the plankton, attaining a large size before metamorphosing and evidently remaining for some time as veligers. Several of them are common at Plymouth. It can be shown that the two groups, containing Mangelia on the one hand and Philbertia on the other, can be distinguished easily by the larval shell, the apex of the one being smooth and of the other elaborately sculptured, and these embryonic whorls still show on the adult. The larval animal is also different in the two groups. *Mangelia nebula*, the commonest species of the genus at Plymouth, is found to have a peculiar gauzy velum which in the later stages envelops the animal and shell like a true veil, quite unlike any form so far seen or described. The velum is ornamented with orange spots, whereas in the true Philbertias the velum is colourless. In *Philbertia gracilis* which is included in a separate sub-genus, the larva has very long velar lobes, with orange spots and a sculptured shell unlike the true Philbertias. All the other Philbertias have similarly sculptured larvæ and are very closely related. All the five British species occur at Plymouth and can be recognised by the embryonic whorls which are all of the same pattern. The larvæ of three of them have been found in the plankton and kept until metamorphosis. The eggs of *Mangelia nebula*, *Philbertia gracilis* and *P. linearis* have been obtained in plunger-jars.

Most of the Rissoidæ also occur in the plankton as veligers of a fair size and in large numbers. There is always a species of Rissoa or its allies in the plankton throughout the year, different species at different seasons. Some are even more abundant in winter than in spring and summer. By keeping the adults it has been possible to obtain the eggs of eight species, six of which have the typical sessile lens-shaped egg-capsules with a long veliger stage and two have single eggs, the larvæ emerging from the capsule in the crawling stage. One Rissoa has a planktonic egg-capsule with one egg. This has not yet been obtained from the animal itself, but gives rise to a veliger which remains long in the plankton and is one of the most important species in winter and early spring. Many of the later stages of this genus can now be distinguished.

An unusual occurrence in the September plankton near the Eddystone was three specimens on separate dates, of the last larval stage of *Dromia vulgaris*, the first record of the larva from Plymouth, although adults are occasionally found. One of them changed to a megalopa in the Laboratory. With the specimens obtained from the eggs in 1931 it has been possible to find the sequence of the larval stages. These larvæ show a complete difference from the Brachyura in almost every important point and fully justify the removal of Dromia from that group. A paper on the subject is now ready and will be published shortly by the Zoological Society.

Mr. D. P. Wilson's work on the development of *Branchiomma vesiculosum* has been continued. Sections of all stages have given interesting information, especially with regard to the metamorphosis, that from external examination only was difficult to bring into line with what is known of other species. During the summer larvæ were again reared and additional knowledge, particularly of the tube-building habits of the newly metamorphosed worms, was gained.

Audouinia tentaculata has been reared from artificially fertilised eggs to an age of three months, when the young worms were growing several of their long branchiæ and had attained most of their adult characters. The development is in the main very straightforward, the trochosphere elongating and acquiring several segments, but bristles are not formed until after metamorphosis. The prototroch disappears gradually, evidently by internal absorption.

The early stages of *Pectinaria koreni* have been obtained from an artificial fertilisation for the first time. They are extremely small, being little more than 60 μ long. Even so they possess a complicated ciliation and have already the great lateral lips characteristic of the Pectinaria larva.

Great efforts have been made to rear *Nephthys hombergi*. Good cultures of the trochospheres are easily got but they have never lived longer than a fortnight and have never formed segments.

Fauna of the Sea Floor (*Ecology, Physiology, Genetics*).

Mr. D. P. Wilson has made a preliminary examination of the micropolychæte fauna of the Eddystone Shell-gravel that has yielded some interesting unrecorded species, amongst them *Jasmineira caudata* Langerhans present in considerable numbers, and *Sphærosyllis bulbosa* Southern.

In collaboration with Mr. J. H. Day of Liverpool, Mr. Wilson has made some observations on the influence of the substratum on the metamorphosis of *Scolecolepis fuliginosa*, the development of which Mr. Day was studying. As had been shown for the Mitraria larva of *Owenia fusiformis*, the character of the bottom played an important part in inducing or delaying metamorphosis. On a muddy sand, such as the adults inhabit, ripe larvæ metamorphosed readily; on a clean sand metamorphosis was delayed for several weeks.

Dr. L. E. Bayliss has been studying the digestive enzymes of the plaice (*Pleuronectes platessa*). This fish has been shown to possess a true anatomical and physiological stomach—unlike some other teleostean fishes—which is capable of secreting a pepsin-like enzyme and the acid necessary to bring the substrate to the required hydrogen-ion concentration. Like most teleosts, the plaice possesses no distinct pancreas, and enzymes similar to those in the mammalian pancreatic juice are secreted by the mucous membrane of the intestine; a trypsin, an erepsin, a lipase, and an amylase have been identified, and alkali can be secreted in order to neutralise the acid from the stomach. There is some evidence that the trypsin is secreted more particularly in the region of the pyloric cæca; this is of interest in view of the histological identification of pancreatic tissue attached to the outer walls of the cæca. Bile, as obtained by slitting open the gall-bladder, contains a trypsin-like enzyme, which is activated by extracts of the intestinal mucous membrane; if, however, the outer surface of the gall-bladder—containing pancreatic tissue—be killed by immersion in a fixing reagent beforehand, the bile appears to be free from enzymes (*cf.* Mackay on Fundulus). The bile, also, has the normal accelerating action on the digestion of fats by the intestinal lipase.

During July, Dr. L. E. Bayliss was co-operating with Dr. and Mrs. Lythgoe on the measurement of the spectro-photometric absorption curves of the visual purple of certain marine fishes (dogfish, ray, conger, gurnard, dragonet, wrasse, plaice, pollack and mackerel). These measurements were made on a specially constructed photo-electric spectro-photometer. Unlike the land animals (frog, rat, man), all of which have an absorption maximum at a wave-length of 505 $m\mu$, and the fresh-water fishes, all of which have an absorption maximum at about 540 $m\mu$, no two of the marine fishes appear to have an absorption maximum at the same wave-length, although they all lie between 505 $m\mu$ and 540 $m\mu$. There appears to be no correlation between the position of the absorption maximum of the visual purple and the habits of the fish, the structure of its eye, or its generic relationships.

Dr. Bayliss has also collaborated with Mr. S. L. Cowan in constructing an amplifier and oscillograph in order to extend Mr. Cowan's researches on the effect of veratrine and yohimbin on the action potentials of the nerve trunks of the walking legs of the spider-crab (*Maia squinado*), the galvanometer used previously having insufficiently rapid time relations. It was found that the last two stages of the amplifier, if arranged in a paraphase-fed push-pull circuit, could be driven from the mains with only negligible distortion, so that a large high-tension battery was unnecessary. Normal nerves appear to contain two sets of fibres, in which impulses are conducted with very different velocities, the whole action potential complex lasting 1/10th to 1/20th sec. The long-continued retention of action potential previously observed as a result of poisoning the nerve with veratrine has been shown to start simultaneously with the true action potential, and to reach its maximum within ½ sec. If single shocks are given whilst the nerve shows a considerable retention—i.e. during the earlier part of the 20 minutes necessary for its complete recovery—apparently normal action potentials can be obtained, without any further increase in the retention. During the earlier part of the retention, small rapid potential waves are observed, whose origin is unknown. A very much more rapid positive after potential which occurs as a result of poisoning with yohimbin, has been shown to occur immediately after the more rapid part of the normal action potential complex, and sometimes is masked by being superimposed on the slower portion of the normal complex. This positive after potential lasts about 1/10th sec.

A paper has been published by Mr. G. M. Spooner giving the results of various investigations, referred to in last year's Report, on the light-responses of marine plankton. It is shown that orientation in the direction of the light-rays is an all-important feature of the behaviour shown in the laboratory, so much so that it is undoubtedly of great significance under natural conditions, in so far as the animals under those circumstances respond to light. The correlation that is found between the distribution of populations in the sea and the light intensity of the surroundings is undoubtedly in a large measure the result of this kind of behaviour on the part of individuals. A start has been made on following up some of the lines of investigation suggested by the above paper ; and data are being collected from various scattered sources on the effects of different light-intensities on the behaviour and physiological activities of animals.

The collection of data bearing on the question of the origin of recessive characters in *Gammarus chevreuxi* which Mrs. E. W. Sexton and Miss A. R. Clark commenced last year has been continued. For various reasons the task has proved to be more laborious than was at first anticipated, but the results which have been obtained have, in the opinion of the workers, more than justified the time spent in making the observations. The number of abnormal eyes which have occurred in breeding from new stocks collected at Chelson Meadow has been considerable, and clearly in excess of the number found previously in similar experiments during the twenty years that the work on Gammarus has been in progress. Perhaps the most interesting of these abnormal-eyed animals is one in which the eyes are of different colours, jet-black on the left side and bright red on the right. Subsequent breeding experiments with this animal have shown that it is heterozygous, although the proportions in which blacks and reds have been obtained from certain of its matings have been unexpected.

Fish and Fisheries.

In last year's Report, reference was made to the preparation by Mr. E. Ford of a comprehensive account of the different branches of herring research which he has conducted and reported on in this Journal in a series of papers entitled : " Herring Investigations at Plymouth." This account was completed and published in August, and represents an endeavour to show the essential bearing of the many seemingly distinct subjects of study upon the problems of the commercial fishery. It concludes with a consideration of the question of forecasting the yield of the fishery from information gathered in preceding years.

In continuation of past practice, Mr. Ford followed the progress of the drift-net fishery for herrings at Plymouth during the winter of 1932–33. The season proved of unusual interest, both with regard to the quality of the fish landed and the quantity caught from day to day. Large fish were greatly in evidence and it appeared that the fishable shoals had come more from westerly sources than had been the case for a number of years. Bulk catches, however, were made only during two short periods, fishing at other times being disappointingly light. Nearly one-half of the season's catch was landed during the seven days from December 12th to 18th., and a further one-sixth in the three days from January 4th to January 6th. The many fishermen, who were not fortunate enough to share in these heavy landings, had a bad season. Much significance is attached to the fact that each of these periods of good fishing followed hard upon days of strong gales, for it confirms the belief that herrings are in some way affected by the blowing of strong winds, so that fish are caught in great numbers in drift-nets which are set as soon after a gale as is practicable.

Mr. Ford has recently begun an investigation into the morphology and variation of the vertebral column in teleostean fishes. Skeletons of upwards of sixty species occurring in British waters have been prepared for examination. In addition to determining the nature and extent of variation from vertebra to vertebra in the same skeleton, from individual to individual in the same species, and from species to species, it is intended to enquire into the probable causes of the variation. First results have already raised interesting questions regarding the relation of form to function and phylogeny. They also have an important bearing upon the problem of races in fishes.

Mr. G. A. Steven has carried further his researches on the rays and skates of the western area of the English Channel, his attention having been devoted chiefly to *Raia clavata*, the most important species commercially. The post-embryonic life of a ray falls into three well-marked stages or phases: (1) the *juvenile* phase, during which the fish simply grows in size; (2) the *adolescent* phase, during which fundamental changes take place very rapidly, and bring the individual to puberty; and (3) the *adult* (sexually mature) phase. The following conclusions have been reached with regard to the growth and maturation of *Raia clavata* in the English Channel. (1) In any sample of male fish of this species in which no fish exceeds about 50 cm. in disc width the majority of individuals will be immature juveniles. This holds good whether the sample be restricted to any arbitrary size group within this range or consists of fishes at all sizes up to 50 cm. (about) maximum. In samples of small range size groups, those groups at the lower end of the range will consist of 100% juveniles, whilst those at the upper end will contain the smallest proportion of juveniles, but this will always remain *above* 50%: (2) similarly, in any sample which includes no fishes less than approximately 55 cm. in disc width, the majority of individuals will be mature adults: (3) in any sample of male fish of size groups falling between about 50 cm. and 55 cm. juveniles and adults will be approximately equally represented and adolescents at all intermediate stages will be found. In the females, which grow to a much larger maximum size than the males, these phases extend over quite different size ranges, the corresponding critical sizes being about 65 and 70 cm. respectively. From the data collected it would further appear that the onset of the changes characteristic of the adolescent period takes place during one growing period and that those changes are completed during the growing period of the following year.

The investigation into the food of Shags and Cormorants which Mr. Steven has been carrying out on behalf of the Cornwall Sea Fisheries Committee has been completed and a final report submitted to the Committee. The substance of this report was published in the Journal of this Association, Vol. XIX, No. 1. The results of the investigation have proved to be most useful and interesting. They have shown very clearly that Shags do not prey to any appreciable extent upon food fishes of any kind, but that Sand Eels and other non-marketable species form their main food. Cormorants, on the other hand, feed largely upon flatfishes and other commercial kinds. It is a grave mistake, therefore, to fail to discriminate between these two birds, more especially as the harmless Shag is fully ten times as numerous as the destructive Cormorant.

At the request of the Ministry of Agriculture and Fisheries, Mr. Steven has carried out an investigation into the complaints which are being made by fishermen along the North Cornwall coast concerning the havoc wrought by Seals amongst their several fisheries, and especially the herring fishery. They complain that the Seals haunt the herring nets and remove the herrings from them. As a result of his investigation, Mr. Steven found that Seals are very numerous on the North Cornwall coast, that the commonest species is the Great Grey Seal (*Halichœrus grypus*) and not the ordinary Brown Seal (*Phoca vitulina*), that the former haunt the nets of the herring fishermen, and that their diet includes herrings. It was quite impossible, however, with the means at disposal, to determine definitely whether the Seals which haunt the nets do so for the purpose of robbing them or simply in order to pick up the fishes which normally fall out of the meshes and are lost.

At the invitation of Colonel E. T. Peel, Mr. F. S. Russell spent in July three weeks of his summer holiday cruising in northern waters in the yacht *St. George*. This cruise, which was primarily made to study the occurrence of the Tunny, *Thunnus thynnus* L., in the North Sea was subsequently extended to cover a period of a further five weeks. The Shetlands and Faeroe Islands were visited and a large number of surface drift bottles were liberated for the Scottish Fishery Board at thirty-mile intervals across the Faeroe Shetland channel. Water samples were also taken from different depths and collections of plankton made. Mr. Russell also assisted Mr. F. C. Fraser in the collection of specimens for the British Museum (Natural History).

In the search for Tunny many fishing vessels of different types were boarded at sea and many hours spent in watching the various kinds of gear at work and examining the catches. The Tunny were eventually located on the northern edge of the Dogger Bank and the first fish caught on August 4th, from which date onwards a number of fish were caught. It is not known whether the Tunny of the Mediterranean and those of the Atlantic are a homogeneous population or whether they can be shown to consist of two or more races. In 1931 at a joint meeting of the International Council for the Exploration of the Sea and the International Commission for the Exploration of the Mediterranean it was decided that a number of body measurements should, if possible, be made on Tunny from different areas to see whether biometric data might give any indication of constant variation between fish from different areas. This cruise afforded the opportunity of making the necessary measurements and thirty-two large fish from the North Sea were examined. Few observations have been published as yet from elsewhere and it is too early to understand the significance of the data obtained, as the results appear to be complicated by change in body proportions with growth. Samples of vertebræ were also taken from a number of fish for a study of age, and at many positions in the North Sea water samples were collected to throw light on the distribution of the Tunny in relation to the hydrographical conditions of its environment.

The weekly observations on the occurrence of young fishes in the plankton at Plymouth are being continued by Mr. Russell in connexion with his general study of the changes in the plankton from year to year.

Work of immediate financial benefit to the fishing industry has been carried out by Dr. Atkins in connexion with the preservation of nets and ropes and advice on these matters has been given to a number of firms. It has been shown, for example, that under standard conditions for rotting untreated netting lasted five months, re-treated with cutch every 2–3 months the netting lasted about two and a half years, but with cutch and a cheap form of copper dip, when re-treated every four months, the netting has lasted seven years. One firm is said to have an annual bill of £5000 for cutch. Using various copper-soap mixtures, with tar, the initial cost of preservation is higher than for cutch, but a single treatment may keep the string sound for from three to four and a half years. For ropes correspondingly good results may be expected and one copper-soap preparation has been found to penetrate rapidly. When kept under Plymouth Pier the preservatives are all relatively less efficient owing to the rapid current and wave action. In practice nets are not kept immersed, save pound-nets, but they rot while damp unless treated with preservative.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated. A special donation from Mr. E. T. Browne has made it possible to add a number of valuable books to the Library.

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Finance.

The Council have again to express their thanks to the Development Commissioners for their continued support of the Plymouth Laboratory. They are grateful also for generous grants from the Fishmongers' Company (£600), the Royal Society (£50), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol (£25), Birmingham (£15 15s.), Manchester (£10 10s.), Leeds (£10 10s.), Sheffield (£5 5s.), the Imperial College of Science and Technology (£10), and the Cornwall Sea Fisheries Committee (£25).

The Council has also to express its thanks to Mr. E. T. Browne for a special donation of £100 to be spent partly on books for the Library and partly for improvements to the store.

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Prof. E. W. MacBride, D.SC., F.R.S. (Zoological Society).
Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society).

List of Annual Subscriptions

Paid during the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
E. J. Allen, Esq., D.SC., F.R.S.	1	1	0
Aquario Vasco da Gama	1	1	0
J. W. Arbuthnot, Esq.	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S.	1	1	0
Miss D. Atkins	1	1	0
Prof. J. Barcroft, F.R.S.	1	1	0
W. H. Barrett, Esq.	1	1	0
L. C. Beadle, Esq.	1	1	0
R. L. Beauchamp, Esq.	1	1	0
G. R. de Beer, Esq.	1	1	0
J. Bělehrádek, Esq., M.D.	1	1	0
Birkbeck College	1	1	0
W. Birtwistle, Esq.	1	1	0
H. H. Bloomer, Esq.	1	1	0
H. Moss Blundell, Esq.	1	1	0
Mrs. H. Moss Blundell	1	1	0
Captain R. J. B. Bolitho	1	1	0
L. A. Borradaile, Esq., SC.D.	1	1	0
Prof. C. L. Boulenger	1	1	0
Col. Sir Henry Bowles, Bart.	1	1	0
A. Bowman, Esq., D.SC.	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
Miss B. L. Boyle (1934 and 1935)	2	2	0
Sir J. Rose Bradford, Bart., K.C.M.G., M.D., D.SC., F.R.S.	1	1	0
J. M. Branfoot, Esq. (1931–1933)	3	3	0
Brighton Public Library	1	1	0
L. R. Brightwell, Esq. (1932 and 1933)	2	2	0
Bristol University (Department of Zoology), 1933 and 1934	2	2	0
Miss E. M. Brown	1	1	0
R. Brown, Esq.	1	1	0
Dr. H. O. Bull (1932–1934)	3	3	0
R. H. Burne, Esq., F.R.S.	1	1	0
M. Burton, Esq.	1	1	0
R. R. Butler, Esq.	1	1	0
Carried forward	43	1	0

	£	s.	d.
Brought forward	43	1	0
E. Bushra, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Prof. H. Graham Cannon, SC.D.	1	1	0
J. N. Carruthers, Esq., D.SC.	1	1	0
Paymaster-Captain R. Charles, R.N. (retd.)	1	1	0
Dr. J. Clark	1	1	0
Coastguard and Fisheries Service, Alexandria	1	1	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
H. A. Cole, Esq.	1	1	0
J. S. Colman, Esq.	1	1	0
Sub.-Lieut. R. Connell, R.N. (1933 and 1934)	2	2	0
Col. R. Stapleton-Cotton, D.S.O. (1934 and 1935)	2	2	0
L. R. Crawshay, Esq.	1	1	0
Miss. D. R. Crofts	1	1	0
F. M. Davis, Esq.	1	1	0
B. Dawes, Esq., D.SC.	1	1	0
Director of Agriculture and Fisheries, Travancore	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
F. M. Duncan, Esq. (1932 and 1933)	2	2	0
Miss N. B. Eales	1	1	0
P. Eggleton, Esq., D.SC.	1	1	0
George Evans, Esq. (the late)	1	1	0
Prof. C. Lovatt Evans, F.R.S.	1	1	0
G. P. Farran, Esq.	1	1	0
Miss R. Fellowes (1933 and 1934)	2	2	0
Prof. R. A. Fisher, SC.D., F.R.S. (1932 and 1933)	2	2	0
E. Ford, Esq.	1	1	0
Dr. G. Herbert Fowler	1	1	0
C. L. Fox, Esq.	1	1	0
Dr. E. L. Fox	1	1	0
Prof. H. Munro Fox	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
F. C. Fraser, Esq.	1	1	0
Prof. F. E. Fritsch, F.R.S.	1	1	0
Prof. J. Stanley Gardiner, F.R.S. (1933 and 1934)	2	2	0
Ghardaqa Marine Laboratory	1	1	0
S. G. Gibbons, Esq. (1931 and 1932)	2	2	0
Prof. E. S. Goodrich, D.SC., F.R.S.	1	1	0
Carried forward	91	7	0

	£	s.	d.
Brought forward	91	7	0
Alastair Graham, Esq.	1	1	0
David H. Graham, Esq. (Balance)		6	1
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq.	1	1	0
Dr. A. M. H. Gray	1	1	0
J. Gray, Esq., M.C., SC.D., F.R.S. (1928–1934)	7	7	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq.	1	1	0
Ian I. Hamilton, Esq.	1	1	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
C. B. Harmsworth, Esq. (1931–1933)	3	3	0
Prof. L. A. Harvey	1	1	0
G. T. D. Henderson, Esq., D.SC.	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq. (1932–1934)	3	3	0
Prof. Sidney J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
Prof. K. Hirasaka (1932 and 1933)	2	2	0
Prof. A. D. Hobson (1931–1933)	3	3	0
Dr. E. G. Holmes	1	1	0
F. R. Horne, Esq.	1	1	0
N. H. Howes, Esq.	1	1	0
P. Hoyte, Esq.	1	1	0
Hull University College	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
Independent Biological Laboratories (Tel Aviv), 1933 and 1934	2	2	0
Miss M. Jepps	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., SC.D., F.R.S.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
J. A. Kitching, Esq.	1	1	0
Dr. G. Lapage	1	1	0
Prof. R. D. Laurie	1	1	0
A. G. Lowndes, Esq.	1	1	0
Adrian Lumley, Esq.	1	1	0
Carried forward	146	5	1

	£	s.	d.
Brought forward	146	5	1
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Prof. D. L. Mackinnon, D.SC. (1933 and 1934)	2	2	0
G. I. Mann, Esq.	1	1	0
B. J. Marples, Esq.	1	1	0
Sir John D. Marsden, Bart.	1	1	0
D. J. Matthews, Esq.	1	1	0
C. A. Mawson, Esq.	1	1	0
Capt. W. N. McClean	1	1	0
C. R. McKenzie, Esq.	1	1	0
Milford Haven Trawler Owners and Fish Salesmen's Association Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Dr. G. A. Millikan	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.SC., F.R.S.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerji	1	1	0
National Museum of Wales, Cardiff	1	1	0
Miss G. L. Naylor	1	1	0
M. H. Neale, Esq. (1934–1935)	2	2	0
Messrs. Neale and West Ltd.	1	1	0
Dr. A. G. Nicholls	1	1	0
J. N. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Dr. C. L. Oakley	1	1	0
Office Scientifique et Technique des Pêches Maritimes	1	0	0
Charles Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC. (1932–1933)	2	2	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock & Buchan, Ltd.	1	1	0
Pease Laboratories Incorporated	1	1	0
Prof. E. Percival	1	1	0
L. E. R. Picken, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
Carried forward	189	5	1

	£	s.	d.
Brought forward	189	5	1
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
W. Proctor, Esq.	1	1	0
Dr. H. E. Quick, M.B., B.S.	1	1	0
Dr. A. Ramalho	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
E. A. Robbins, Esq. (1933 and 1934)	2	2	0
V. Rothschild, Esq.	1	1	0
C. H. Rudge, Esq. (1934 and 1935)	2	2	0
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
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J. T. Saunders, Esq.	1	1	0
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Miss Lilian Sheldon	1	1	0
C. J. Shen, Esq.	1	1	0
Prof. W. Rae Sherriffs, D.SC.	1	1	0
H. P. Sherwood, Esq.	1	1	0
B. Webster Smith, Esq. (1932, 1933 and part 1934)	2	12	6
F. G. W. Smith, Esq. (1932 and 1933)	2	2	0
Prof. E. A. Spaul	1	1	0
G. M. Spooner, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	3
Prof. T. A. Stephenson, D.SC.		18	6
Mrs. N. S. Steven	1	1	0
Eric J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Carried forward	234	16	4

	£	s.	d.
Brought forward	234	16	4
Harold Thompson, Esq., D.SC.	1	1	0
Sir Herbert F. Thompson, Bart.	1	1	0
Torquay Natural History Society	1	1	0
Phillip Ullyot, Esq.	1	1	0
R. C. Vernon, Esq.	1	1	0
H. M. Vickers, Esq.	1	1	3
Dr. A. Walton	1	1	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
Mrs. F. J. Weldon	1	1	0
A. E. J. Went, Esq.	1	1	0
Miss K. M. White	1	1	0
P. H. F. White, Esq.	1	1	0
D. P. Wilson, Esq.	1	1	0
Mrs. D. P. Wilson, PH.D.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
Total	£255	16	7

List of Donations to the General Fund

For the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
D. L. Bryce, Esq.	1	1	0
G. I. Mann, Esq.		10	6
B. G. Wilson, Esq.		7	6
Total	£1	19	0

Special Donation for Improvements to the Store and for the Library

Paid during the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
E. T. Browne, Esq.	100	0	0
Total	£100	0	0

List of Composition Fees

Paid during the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
Dr. L. H. N. Cooper	15	15	0
Prof. E. J. Salisbury, D.SC., F.R.S.	15	15	0
	£31	10	0

THE MARINE BIOLOGICAL ASSOCIATION

BALANCE SHEET

	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:						
On Open Account				87	10	8
GRANT RECEIVED IN ADVANCE				150	0	0
JEWISH SCHOLARSHIP FUND:						
First Instalment Received	125	0	0			
Less Expenditure	33	15	10	91	4	2
E. T. BROWNE SPECIAL DONATION FUND:						
Donation Received	100	0	0			
Less Expenditure	74	11	10	25	8	2
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:						
As at 31st March, 1933	763	3	9			
Add: Transfer from Income and Expenditure Account	269	14	2	1,032	17	11
SURPLUS:						
As at 31st March, 1933	5,851	16	0			
Add: Composition Fees	31	10	0			
Surplus for the year as per Income and Expenditure Account	153	18	1	6,037	4	1
				£7,424	5	0

(Signed) M. H. NEALE
R. A. FISHER } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the
Capital expenditure on erection of Buildings on Land held on Lease from the War
Sheet is properly drawn up so as to exhibit a true and correct view of the state of the
given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
Plymouth. *7th April,* 1934.

OF THE UNITED KINGDOM.

31st MARCH, 1934.

	£ s. d.	£ s. d.
BOATS AND EQUIPMENT, as per Valuation as estimated by the Director at 31st March, 1931		
S.S. *Salpa*	2,000 0 0	
Motor-boat	150 0 0	
Nets, Gear and General Equipment	27 0 0	2,177 0 0
LABORATORY APPARATUS, ENGINES AND PUMPS:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost		
As at 31st March, 1933		580 2 10
LIBRARY:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost less Depreciation		
As at 31st March, 1933	2,082 1 2	
Additions during the year	518 14 0	
	2,600 15 2	
Less: Depreciation	467 11 2	2,133 4 0
STOCK OF SPECIMENS, CHEMICALS AND JOURNALS as estimated by the Director		325 0 0
SUNDRY DEBTORS		106 11 10
INCOME TAX RECOVERABLE		22 11 3
PREPAYMENTS		94 6 5
GENERAL FUND INVESTMENTS at Market value as at 31st March, 1931:		
£410 14s. 8d. New Zealand 4% 1943/63	344 15 0	
£352 2s. 3d. Local Loans 3%	232 7 10	
(Market value at date £746 17s. 0d.)		577 2 10
DEPRECIATION FUND INVESTMENTS at Cost:		
£590 6s. 0d. Local Loans 3%	506 10 9	
£533 5s. 8d. Conversion Loan 3%	526 7 2	
(Market value at date £1,078 3s. 5d.)		1,032 17 11
COMPOSITION FEE FUND INVESTMENTS at Cost:		
£18 8s. 6d. Local Loans 3%	15 15 0	
£63 19s. 8d. Conversion Loan 3%	63 0 0	
(Market value at date £81 0s. 6d.)		78 15 0
CASH AT BANK AND IN HAND:		
Coutts & Co.	6 15 6	
Lloyds Bank Limited	253 13 4	
Cash in Hand	36 4 1	296 12 11
		£7,424 5 0

Association and have obtained all the information and explanations we have required.
Department is excluded. Subject to this remark we are of opinion that the Balance
Association's affairs, according to the best of our information and the explanations

(Signed) PRICE, WATERHOUSE & Co.

INCOME AND EXPENDITURE ACCOUNT

	£	*s.*	*d.*	£	*s.*	*d.*
To Salaries, including Institution's Contributions to Superannuation				6,749	7	8
,, Laboratory Wages, including National Insurance and Institution's Contribution to Superannuation				2,121	7	3
,, Depreciation of Library				467	11	2
,, Scientific Publications, *Less* Sales				408	13	10
,, Upkeep of Laboratories and Tank Rooms :						
Buildings and Machinery	171	16	0			
Electricity, Gas, Coal, Oil and Water	317	13	9			
Chemicals and Apparatus	348	12	4			
Rates, Taxes and Insurance	98	16	6			
Travelling	122	19	9			
Stationery, Postage, Telephone, Carriage and Sundries	303	15	5			
Specimens	109	15	10			
				1,473	9	7
,, Maintenance and Hire of Boats :						
Wages, including Diet Allowance, National Insurance and Casual Labour	1,578	16	1			
Coal, Water, Oil, Petrol, etc.	212	5	11			
Maintenance and Repairs with Nets, Gear and Apparatus	612	2	5			
Purchase of Material for Nets for Sale, excluding Labour	248	2	11			
Boat Hire and Collecting Expenses	7	9	2			
Insurance	287	0	11			
				2,945	17	5
,, Transfer to Depreciation Reserve Account				269	14	2
,, Balance being Surplus for the Year				153	18	1
				£14,589	19	2

YEAR ENDED 31st MARCH, 1934.

	£	s.	d.	£	s.	d.
By Grants :						
Ministry of Agriculture and Fisheries, Grant from Development Fund	10,949	7	2			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	25	0	0			
				11,704	7	2
,, Subscriptions				255	16	7
,, Donations				1	19	0
,, Sales :						
Specimens	1,075	9	2			
Fish (*less* expenses)	117	10	5			
Nets, Gear and Hydrographical Apparatus	325	10	7			
				1,518	10	2
,, Table Rent				480	11	9
,, Tank Room Receipts				556	2	5
,, Interest on Investments (*less* Bank Charges)				35	17	4
,, Sale of Dr. M. V. Lebour's Book	4	12	0			
,, Sale of "Marine Fauna of Plymouth"	9	11	6			
				14	3	6
,, Income Tax Recoverable				22	11	3
				£14,589	19	2

THE
QUARTERLY JOURNAL
OF
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EDITOR:
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OBJECTS
OF THE
Marine Biological Association
OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

Professor Huxley, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the Duke of Argyll, Sir Lyon Playfair, Lord Avebury, Sir Joseph Hooker, Dr. Carpenter, Dr. Günther, Lord Dalhousie, Professor Moseley, Mr. Romanes, and Sir E. Ray Lankester.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000 and from that time until 1933 a sum of over £16,000 has been spent on additional buildings. Throughout this period investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the maintenance of a research steamer and other collecting boats, and the salaries of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances.

TERMS OF MEMBERSHIP.

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition Fee	15	15	0
Founders		100	0	0
Governors		500	0	0

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